University of South Bohemia in České Budějovice

Faculty of Science

Modelling of spruce forest decay caused by the European spruce bark beetle in the area of Bohemian Forest using GIS

Master thesis

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Annotation:

This thesis deals with the bark beetle population gradation which resulted in dieback of montane spruce forest in the central part of the Bohemian Forest, Czech Republic, during 1991 – 2000. A spatio-temporal model of changing land cover has been made using remote sensing and GIS methods. The statistical analyses have been made using generalized linear models (GLM). The possible effect of various conditions and environmental factors at landscape as well as the stand level has been discussed.

Prohlašuji, že svoji diplomovou práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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Bc. Zdeněk Brož

Poděkování

Děkuji všem, kteří mi umožnili tuto práci nejen započít, ale také dokončit. Jmenovitě svým rodičům, prarodičům i přítelkyni Šárce. Svým školitelům Martinu Haisovi a Standovi Grillovi děkuji za shovívavé jednání, hlubokou trpělivost, velké nasazení a v neposlední řadě také odborné vedení. Míše, Víťovi, Káďovi i mnoha jiným více či méně anonymním přátelům a kamarádům děkuji za veškerou pomoc, kterou mi nezištně poskytli.

List of contents

1 Introduction

The bark beetles have always attracted the interest of scientists as well as foresters due to their significance in terms of ecological as well as economic impact (Hofstetter & Vega, 2015; Knížek, 2008). The number of so far published scientific sources related to the bark beetles is estimated to be up to 40 thousand (Knížek, 2008). During the last 25 years, however, the topic has attracted also many others. The general attention was induced especially by the recent outbreaks often of unprecedented scale (e.g. Six et al., 2014; Skuhravý, 2002). Moreover, the destructive nature of the bark beetles infestations certainly played an important role as well (Müller, 2011). Extensive diebacks of forests stirred up a conflict between the ecological and the economical point of view and the factual debate has gradually changed into a political issue which has been widely publicized (Flint et al., 2009; Müller, 2011; Skuhravý, 2002). The situation has become confusing and the essence of the problem has often faded away. Will it be better?

No one knows, but one thing is certain. The bark beetles outbreaks have always been an integral part of the forest dynamics at least in Holarctic ecozone (Skuhravý, 2002) and the incidence of the outbreaks will even increase in near future under the conditions of the global climatic change (e.g. Bentz et al., 2010; Müller, 2011). Despite these facts there is still a significant lack of knowledge regarding many questions about the bark beetles ecology and population dynamics (e.g. Wermelinger, 2004). The increasing importance on one side and the incomplete knowledge on the other side are significant motivation stimuli for further research. Perspective seems especially the use of the whole variety of modern methods from molecular biology to satellite imagery that have been largely developed within the new millennium.

When focused on the bark beetles population dynamics and dispersion patterns at the stand or landscape level, the remote sensing and GIS methods seem to be the ideal choice. On one hand they enable to cover the whole outbreak in terms of both – space and time but on the other hand, especially when working with aerial photography, they enable to analyse the data in a fine detail (e.g. Hendert, © 2012).

While the most aggressive bark beetle in the Nearctic region is the mountain pine beetle (*Dendroctonus ponderosae*), the most aggressive species from the Palearctic region is the European spruce bark beetle (*Ips typographus*). Its outbreaks are documented from many European and Asian forests sometimes even several hundred years back into history (Skuhravý, 2002). In conditions of the central Europe and the Czech Republic, it attacks almost exclusively the Norway spruce (*Picea abies*; Tollefsrud et al., 2008). From this perspective, the two national parks – the Šumava National Park and the Bavarian Forest Nation Park situated one next to each other in the Bohemian Forest between the Czech Republic and the Federal Republic of Germany represent the ideal study area of the European spruce bark beetle population dynamics and dispersion pattern (Skuhravý, 2002). This area in fact, constitutes the largest compact area of montane forest in the central Europe, where the Norway spruce is often a dominant species (Neuhäuslová et al., 20011; Skuhravý, 2002).

The study area as defined in this thesis is situated in the central part of the Šumava National Park. It has been chosen because of several reasons. Primarily, it belongs to a non-interventional zone regarding the bark beetle attacks. It is also highly forested while the forests species composition is close to 100 % of Norway spruce (Kindlmann et al., 2012). Another important factor is the existence of annually taken aerial images suitable for purposes of the thesis. Advantage was the fact that the bark beetle research in the Bohemian Forest has already about 30 year's long tradition (Skuhravý, 2002). Finally, the actual occurrence of a large European spruce bark beetle population gradation in nineteen-nineties has been of key importance.

To summarize what has been stated above, there has been significant demand from both the scientific as well as the public domain for extensive European bark beetle research. The ideal situation for such research occurred in the central part of the Šumava National Park during the nineteen-nineties when the population gradation occurred. So the thesis has been elaborated using the remote sensing and GIS methods suitable for such purposes. The results are expected to be valuable from the scientific point of view but they might be useful for nature conservation and forestry as well.

2 Review

2.1 Mountain ecosystems

Mountain ecosystems cover a significant part of the Earth's land. According to various estimates and definitions it's about 12 to 24 % (e.g. Kapos et al., 2000; Körner et al., 2005; Körner et al. 2011). Hand in hand they represent about 25 % of global terrestrial biodiversity and nearly half of world's biodiversity hotspots (Spehn et al., 2010). This remarkable abundance of diversity rises mostly from the so-called mountain phenomenon. Its principle lies in compression of different climatic life zones and different small-scale habitats. Climatic life zones are changing gradually with the altitudinal gradient whereas differentiation of mountain habitats is primarily caused by existence of different topoclimates, their isolation and fragmentation and pressure of moderate disturbances (Körner, 2004; Spehn et al., 2010).

In a few words – the heterogenic nature of mountains creates an extremely wide spectrum of different environments and life conditions leading to an extraordinary diversity of organisms. For many of them, mountains represent their cradles or refuges. For others, they are migration barriers or corridors (Spehn et al., 2010). Apart from this level, mountains have also many general ecological functions – most importantly they play an essential role in climate formation and water cycle (Price, © 2016).

Because of these reasons, mountains represent areas of great natural value and therefore are in forefront of present nature conservation interests. However, the reasons are much wider. Billions of people depend on mountains either directly or indirectly. For example more than half of the mankind uses the water which is captured, stored and purified in mountains. At the same time less than quarter of these people live directly in the mountainous regions (Huddleston & Ataman, 2003). Besides that, mountains provide us with many other goods and services either based on provisioning (e. g. hydropower, timber), regulating and supporting (e. g. watershed and hazard prevention, soil fertility, soil as storage reservoir for water and carbon) or even on cultural (e. g. cultural and ethnological diversity) basis (Grêt-Regamey et al., 2012).

No wonder that more than half of the world's natural protected areas are in mountains, including 40 % of all biosphere reserves (UNSECO-MAB, 1996). On the other hand, mountain ecosystems are not only one of the most protected but also one of the most endangered and fragile environments. Montane moist forests are according to Whitmore & Sayer (1992) being deforested even faster than tropical rain forests for instance.

2.1.1 Mountain (montane) forests

Forests and woodlands are the most common type of ecosystems in mountain regions. According to Olson et al. (2001), they cover nearly half of the mountainous area in global. There are many global classification systems of forests in use but none of them has been universally accepted (Jenkins & Groombridge, 2002). One of the simplest but most potent classification systems brought by UNEP-WCMC (2009) is based on reclassification of 26 major forest types to 6 broader categories with similar combinations of climatic zones and principal types of trees in common. These categories are:

- Temperate coniferous forests,
- Temperate broadleaved and mixed forests,
- Tropical moist forests,
- Tropical dry forests,
- Sparse trees and parkland,
- Forest plantations.

Each of these categories is also commonly represented in mountains at some parts of the world.

2.1.1.1 Mountain tree line & climatic belts

Most of the mountain forests can be found in the lowest elevations between 300 and 1000 m whereas at heights above 4000 m there are almost no trees worldwide (Kapos et al., 2000; Körner, 2003). This ecological limit is known as the mountain treeline and is an analogy to a polar limit. On a large scale, both mountain and polar tree limits are set by temperature during the growing season. It´s part of a common knowledge that temperature decreases with higher altitudes and latitudes respectively. Because of this general rule, the treeline is at its highest elevations in equatorial regions and goes down towards the poles ending on the polar limit near the sea level (Körner & Paulsen, 2004; Ohsawa, 1990).

Although trees don´t always reach their potential climatic limits (Körner, 2003), the mountain tree line described above is traditionally used to define the border between two ecologically different mountain belts – montane and alpine. The most significant difference is just at the presence or absence of regular forests. Above the alpine belt also nival belt can be formed. It is defined as an area above the line of permanent snow (Körner, 2003). For graphical representation see Figure 1.

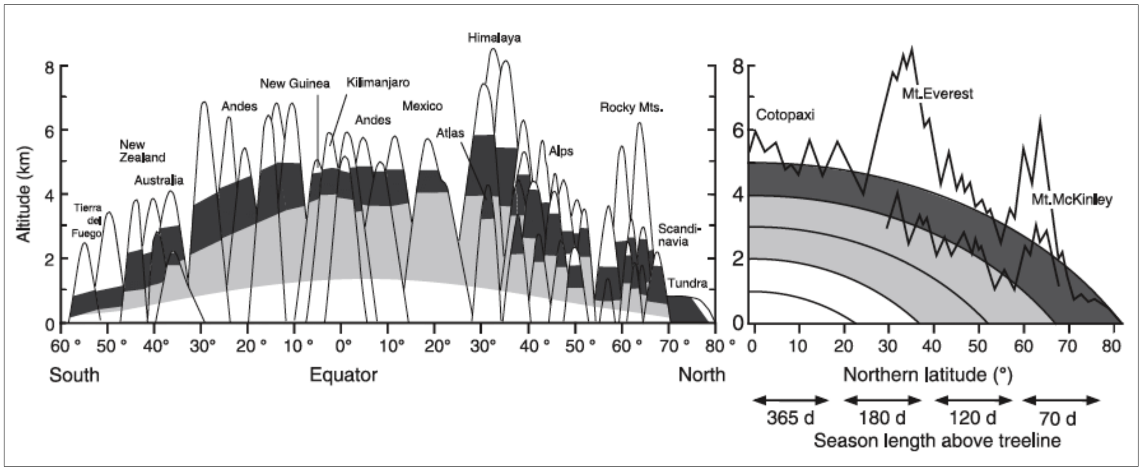

Figure 1: Image representing the classical Humboldt profile taken from Körner (2003).

Description: The figure shows latitudinal position of altitude belts in mountains across the globe and compression of climatic life zones on mountains; altitude for latitude. Grey colour represents montane, black alpine and (upper) white nival belt.

2.1.1.2 Dynamics of montane forests

As stated above, it's primarily a unique combination of mountain topography and climate what determines the environmental conditions of montane forests. On one hand montane forests represent a unique type of forest ecosystems and for sure the specificities of mountains can lead to acceleration and amplification of their dynamics. On the other hand, the nature of these dynamics remains unchanged and it is based on the same principles as in lower altitudes (Lindenmayer et al., 2008).

Disturbances

According to current and commonly accepted paradigm described e. g. by Frelich (2002), a typical forest ecosystem is a subject of constant change. Drivers of this change and therefore key ecological processes in most of the forest ecosystems worldwide are natural disturbances (Frelich, 2002). Of many definitions available I chose the one suggested by Lindenmayer et al. (2008): disturbance is an event more or less discrete in time and space that causes mortality of the dominant vegetation which results in habitat alternation and release of resources.

The definition implies that disturbances exist at different spatial and temporal scales that must logically overlap in spatio-temporal continuum (Kuuluvainen, 2002). Therefore the dynamics (or stability) of montane forest in terms of structure and species composition is a question of chosen scale (Frelich, 2002). Traditionally, the spatial dimension is more emphasized and three basic scales are usually distinguished (Frelich, 2002):

- Patch level (approx. 0.01 – 0.1 ha),
- Stand level (approx. 1 – 10 ha),
- Landscape level (approx. 1 000 - 1 000 000 ha).

The problem of scale, however, is generally one of the principal problems in ecology and many authors define these scales in different ways or use levels of their very own.

Definitions of temporal scales are generally even more variable. On the other hand, they actually relate to spatial scale and also severity scale classifications more or less (Bunnell & Huggard, 1999; Frelich, 2002). For example, gap forming disturbances that affect only individuals or small groups of trees (i.e. patch level) are of relatively low intensity but high frequency. High-intensity disturbances in contrast, normally occur less frequently and principally at landscape level, wherefore they significantly affect the whole forest (Lindenmayer et al., 2008).

Disturbance regimes

The spatio-temporal continuum of disturbances is much more complicated though. Disturbance dynamics are affected by many different factors, such as climate (or even extreme weather), geomorphology, soils, species composition, etc. (Kuuluvainen, 2002). According to type and character (expressed in terms of disturbance agents, intensity, severity, extent, frequency etc.) of all the disturbances, we speak about different disturbance regimes (Frelich, 2002; Lindenmayer et al., 2008).

In long term, disturbance regimes form the overall character of a particular forest landscapes primarily by changing their biotic components (forest structure and composition). They are decisive for proportions of stands of various stages of development on landscape level as well as the composition of patch mosaic at stand level (Frelich, 2002).

Succession

The opposite side of forest dynamics is represented by successional processes. These are of equal significance as processes described above and many disturbances actually couldn’t occur without these contradictory forces (Kuuluvainen, 2002). Both types of processes are closely connected since disturbance characteristics usually strongly affect the successional development which comes afterwards and vice versa (Kuuluvainen, 2002).

2.1.1.3 Montane forests in central Europe

All general facts about mountains and montane forests that have been stated above can be successfully down-scaled from the global level up to the regional level and applied to conditions of central Europe, and the Czech Republic respectively.

The highest mountain ranges in Czech Republic are Ore Mountains, Giant Mountains, Sudetes and Bohemian Forest (Vacek et al., 2012). All of these ranges are situated in border areas at periphery. It's not a coincidence that the majority of national parks and protected landscape areas have been established at the same areas. Most of them abound with significant forest cover. Although their natural character has been largely changed, forests especially in special protected areas have preserved their natural vertical stratification to some extent (Vacek et al., 2002).

Czech mountain forests classification system

Czech forest classification system in general distinguishes 9 forest altitudinal zones[1] based on distinction of main tree species presence (Viewegh et al., 2003). First altitudinal zone considered to be a mountain forest is the 5th zone – beech with fir. In higher altitudes it's replaced by beech with spruce (6th) and spruce with beech (7th) zone. The so called "upper montane forest zone" (8th) is formed only at highest elevations in mountain ranges named above and consists dominantly of spruces. Distribution of all altitudinal forest zones within Czech Republic is shown in Figure 2.

The upper border of spruce zone is the alpine forest limit as well. The altitude of the limit(s), however, differs depending on the latitude. For example, the difference between Bohemian Forest and Giant Mountains is about 2° in latitude, which represents about 150 m in elevation (Körner et al., 2003). Therefore the mountain tree limit in Giant Mountains is at about 1 250 m whereas in Bohemian Forest it would be at about 1 400 m above the sea level (Prach & Jonášová, 2005). The lower limit of the 9th zone is at about 1 150 m above the sea level in Bohemian Forest (Čada et al., 2013a).

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[1] The extreme 9th (dwarf pine) zone is little bit special in its own way because dwarf pines actually don't create tree forms and therefore are considered to grow above the mountain tree limit.

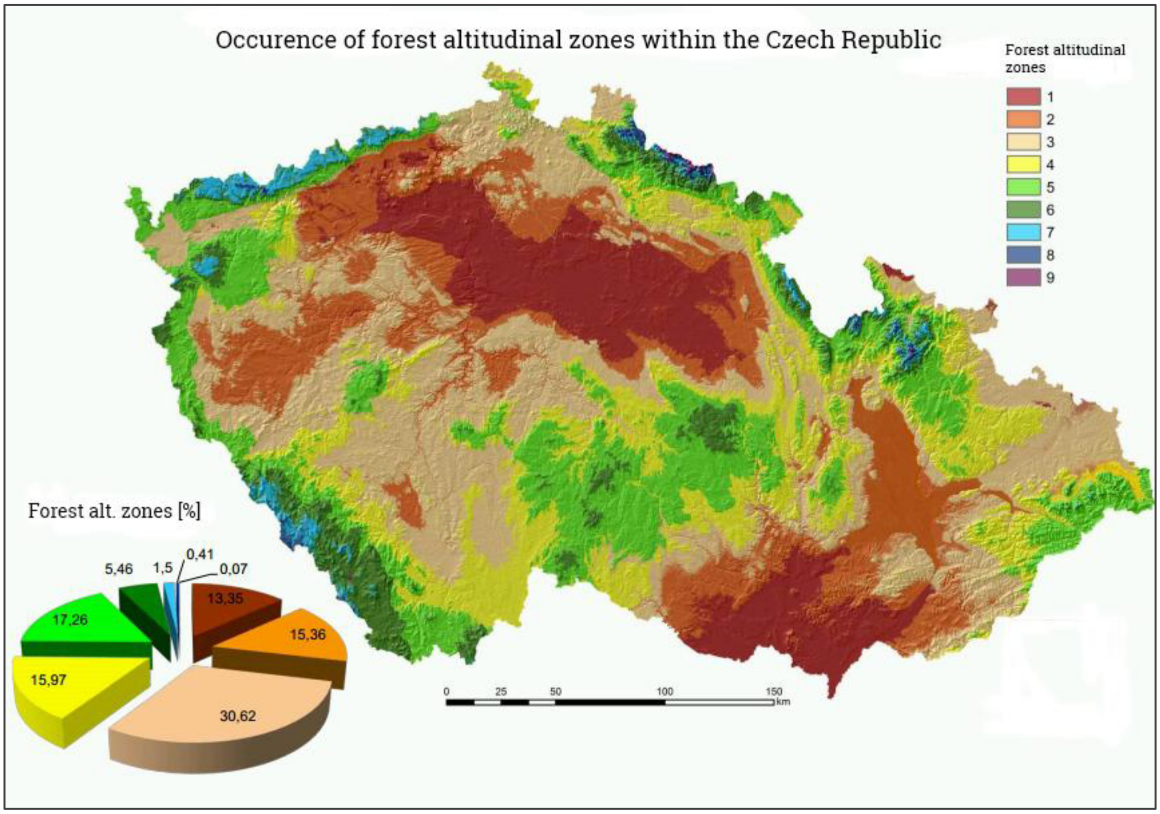

Figure 2: Map of the Czech Republic showing model of present forest altitudinal zones. Taken from Vahalík[2] (© 2012) and modified.

Description: The figure shows individual forest latitudinal zones distinguished by different colours. Spruce (8th) zone, so called upper montane spruce forest, is represented by dark blue colour and according to pie chart stretches over about 0,41 % of the total area.

Dynamics of upper montane spruce forests

Although the parallel between central European montane spruce forests and Scandinavian or North American boreal forests is generally valid, the dynamics are different after all. The main difference is in character of disturbance regimes. Boreal forests often tend to be strongly affected by fires while in central Europe fires have only very limited importance at the expanse of wind (D'Amato et al., 2011; Lilja et al., 2006; Bengtsson et al., 2000). Recent findings also suggest that forest dynamics in Scandinavia are more driven by small-scale gap dynamics rather than large

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[2] Ing. Petr Vahalík – GIS department at Mendel University in Brno. Unpublished data.

disturbances happening at landscape level. This is, in contrast, probably more the case of central Europe (Holeksa et al., 2007; Kuuluvainen, 2002; Kuuluvainen et al., 1998). It does not mean the gap dynamics do not appear in central European montane forests, they just seem to be of lower importance (Svoboda & Pouska, 2008). Anyway, in both types of forest the main disturbance is often followed by insect outbreaks (Schelhaas et al., 2003).

According to scientific mainstream consensus, the main forces driving the ecological processes in mountain spruce forests in central Europe are wind and bark beetle (e.g. Fischer et al., 2002; Schelhaas et al., 2003, Svoboda et al, 2010). Thus current structure and dynamics of present forests are results of these disturbances. However, as shown in Figure 2, the mountain spruce forests in Czech Republic don't cover significantly large areas where these subjects could be thoroughly studied (Svoboda, 2008). For this reason it's necessary to resort to studying of historical sources (e.g. Brůna et al., 2013; Čada et al., 2013a) or indirect methods (e.g. Čada et al., 2013b).

Windstorms

Historical sources dating several hundred years back into past show that windstorms occur in conditions of central Europe relatively often but with varying intensity (e.g. Dobrovolný & Brázdil, 2003). Basically, occurrence of strong winds, that can possibly disturb large stands of forest, can be described as irregular but highly probable in long term. Such windstorm comes probably once in few hundred years according to Svoboda (2008). This statement is in accordance with the report from Munich Reinsurance Company (2002) which notes it can happen in the area of the Bohemian Forest once per 100 years.

Once the windthrow occurs and the forest is significantly weakened, broken or uprooted trees become suitable candidates for bark beetle attack (Skuhravý, 2002). Causal nature of the relationship between windstorms and bark beetle population dynamics has been revealed by Økland & Bjørnstad (2006). List of windstorms and bark beetle infestations documented between 1710 and 1989 in Bohemian Forest was published by (Čada et al., 2013a).

Bark beetle

Most of the time, the bark beetle population exists only at low numbers (Kindlmann et al., 2012). The beetles are able to successfully attack only weak individual spruces and their dynamics doesn’t affect the forest at stand or even landscape level (Skuhravý, 2002). If the conditions become more favourable (e.g. after large windthrow), however, the population can rapidly grow in numbers just within few years (Wermelinger 2004).

Once certain thresholds are crossed, the pressure on spruces is so strong that even healthy trees succumb to bark beetle attack and die (Skuhravý, 2002). Therefore extent of such disturbance is often larger than the original windthrow (Skuhravý, 2002) – in central Europe easily in order of square kilometres (Skuhravý, 2002). On the other hand, bark beetle outbreaks usually don’t last more than few years due to intensification of feedbacks (e.g. pathogens or predators) and lack of food resources (Kindlmann et al., 2012; Skuhravý, 2002). Soon after forest brake-up, released resources enable and accelerate the spontaneous regeneration and the forest returns to its original form (Jonášová & Prach, 2004; Heurich, 2009). It is a question of frequency and intensity of disturbances whether this applies to the whole forest or just some parts.

Forest cycle

As stated above, mountain forests are subjected to a whole spectrum of disturbances from small-scale gap forming events up to large-scale and high-severity disturbances. Whether the large-scale disturbances prevail or not all the disturbances exist in one spatio-temporal continuum (e.g. Svoboda et al., 2012). As a result, mountain forests at landscape level comprise of stands in different states of development from initial stages subjected to secondary succession up to old-growth forests (Kuuluvainen, 2002).

Theoretically, almost every stand will once be subjected to the large-scale disturbance. Therefore it is only question of time whether the stand as a whole will reach the stage of old-growth forest or how long it will remain in that stage (Kuuluvainen, 2002). Different phases of montane forest stand development are shown in Figures 3, 4 & 5.

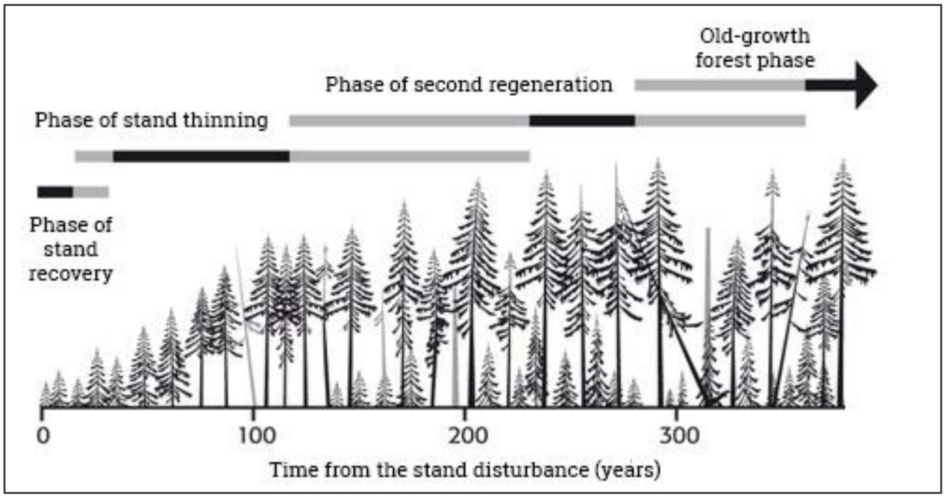
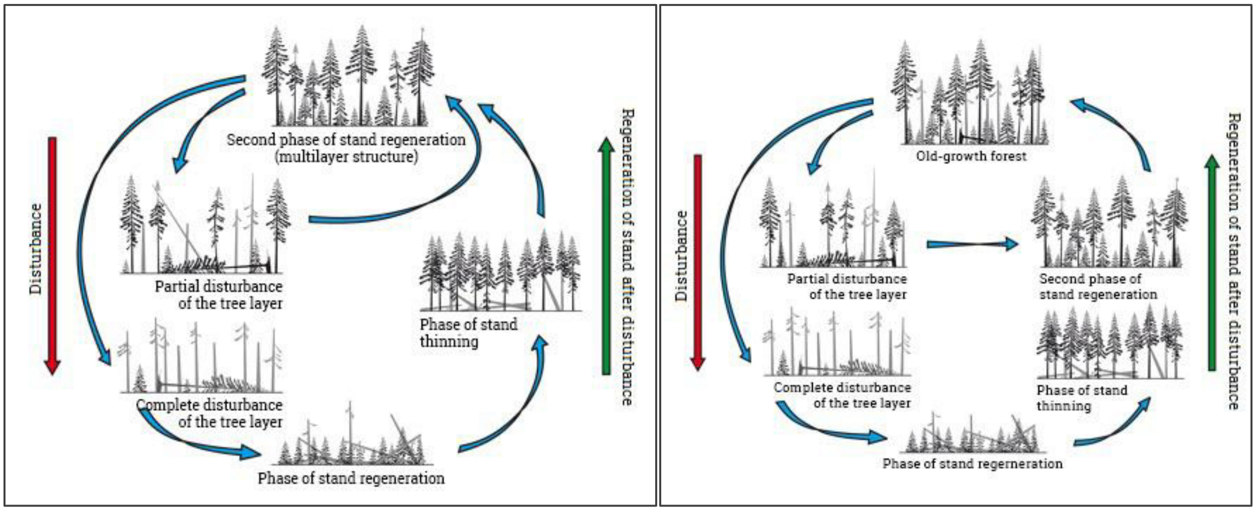


Figure 3: Simplified development schema of montane spruce forest under conditions without large-scale and high-severity disturbances. Taken from Oliver & Larson (1996).

Description: some windthrow or large-scale bark beetle attack causes a dieback of forest. At this point, a new forest is established and slowly develops via the secondary succession. It gradually changes its structure, matures, becomes more complex… and later eventually reaches the old-growth forest phase. It will stay in this phase until it is severely disturbed and "the circle is closed".



Figures 4, 5: Forest development under different disturbance pressures (Svoboda, 2008).

Description: In the first picture the disturbance pressure doesn't allow the forest to reach the old-growth phase of development. Younger stages formed by disturbances of different severity prevail. The right picture shows situation where older stages prevail due to lower disturbance pressure.

2.2 Bark beetles

Bark beetles in broader sense (Coleoptera, Curculionidae, Scolytinae) play a vital role in forest ecosystems all over the world. They are among first decomposers of dying or recently died trees and therefore are considered an important factor in the process of natural forest regeneration. Many of them significantly contribute to creation of dead matter as well as free space which is subsequently utilized by number of insects, fungi, plants and other groups of species (Müller et al., 2008; Raffa et al., 2015).

The subfamily Scolitinae comprises of two basic ecological groups – so called ambrosia beetles that belong to xylomycetophages and phloemophagous beetles, i.e. bark beetles in narrow sense (Woods & Bright, 1992). Based on their feeding strategy, species in the second group can be further divided between monophages and polyphages. Naturally, each of these species prefers different host plants, feeds on different parts of these plants etc. (Raffa et al., 2015). Most of so far described bark beetles prefer dead, eventually under epidemic conditions also weakened hosts, and don't attack healthy plants at all (Rudinsky, 1962). In contrast, it has been reported that probably less than dozen of bark beetle species are, again – under epidemic conditions – able to attack and successfully kill even vital trees (Franceschi et al., 2005). Similarly Raffa et al. (2008) estimate the number of bark beetles capable of broadscale outbreaks to be less than 1 %. These aggressive species can cause dieback of trees on extensive areas especially in artificial forests (Faccoli & Bernardinelli, 2014). Typical genera of such beetles are *Dendroctonus* in North Amerika (Six et al., 2014) and *Ips* in Eurasia (Franceschi et al., 2005; Skuhravý, 2002).

2.2.1 Examples of bark beetle outbreaks

For example, the infestation outbreak of mountain pine beetle (*Dendroctonus ponderosae*, Hopkins 1902) currently ongoing in western USA and Canada had affected the total area larger than 35 million hectares of pine[3] forests with 70 – 90% kill rate in 2013 according to United States Department of Agriculture (© 2016). This makes the outbreak the largest ever documented in human history (Six et al., 2014). Although it seems the infestation finally lingers, another native but invasive species, the spruce beetle (*Dendroctonus rufipennis* Kirby, 1837), currently rises in numbers (United States Department of Agriculture, © 2016).

Across the ocean, the spruce represents a host plant of another aggressive species – European spruce bark beetle (*Ips typographus* Linnaeus, 1758). One of the largest calamities caused by this beetle happened between 1868 and 1878 in former Austria-Hungary. In 1868, severe windstorms caused large windthrows on both sides of Bohemian Forest that were beyond capacities of foresters. Forests full of felled and broken trees created favourable conditions for gradation of bark beetle in following years. Skuhravý (2002) sums that about 9 000 hectares of forest were damaged and more than 3.6 million m^3 of wood was logged. This is probably a conservative estimate, while e.g. Pfeffer (1952) reports salvage logging up to 7 million m^3.

2.2.2 Systematics

According to Woods & Bright (1992) later supplemented by Bright & Skidmor (1997, 2002) and Bright (2014), bark beetles are currently represented by 25 tribes, 225 genera and about 6 000 species worldwide. The classification is not always clear and will probably change in the future, though (Bright, 2014). It's also probable that many other species haven't been discovered yet (Knížek, 2008). Anyway, about 1500 species have been reported from the Holarctic area of which about 900 are from Palearctic area (Knížek & Beaver, 2004). Data related to Europe vary greatly according to geographical definition. Knížek (2004), for example, reports 315 European species. The same author also reports 111 species from Czech Republic (2008) while Kindlmann et al. (2013) report 110 species. One way or another, majority of them (69 species according to Knížek,

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[3] Mountain pine beetles attack various American pine species, namely: *Pinus ponderosa*, *Pinus albicaulis*, *Pinus contorta*, *Pinus sylvestris*, *Pinus banksiana* and *Pinus flexilis* (Erbilgin et al., 2014).

2008) feed on coniferous trees – mostly pine and spruce. These tree genera accompanied by fir are host plants also for genus *Ips* which is represented by 6 different species in Czech Republic (Kindlmann, 2013). Three of them – namely European spruce bark beetle (*Ips typographus*), small spruce bark beetle (*Ips amitinus*) and double-spined spruce bark beetle (*Ips duplicatus*) undertake their development on spruce trees. Their co-occurrence at the same tree is not rare (Zahradník & Knížek, 2007). From ecological as well as economical point of view far most important is the European spruce bark beetle (*Ips typographus* Linnaeus, 1758).

2.2.3 European spruce bark beetle (*Ips typographus*)

The European spruce bark beetle (*Ips typographus* Linnaeus, 1758) is considered to be the most aggressive Eurasian bark beetle (Skuhravý, 2002). In Asia, its larvae and imagoes feed on about 10 different species of coniferous genera. In Europe, however, they inhabit almost exclusively the spruce genus represented mainly by Norway spruce (*Picea abies*, [L.], Karst.). Therefore, widespread of European spruce bark beetle is closely connected with the areal of spruce (Tollefsrud et al., 2008). The species is widespread from south-east Europe up to Far East, where on Japanese islands, the subspecies *Ips typographus* f. *japonicus* is common (Nobuchi, 1974; Skuhravý, 2002).

2.2.3.1 Basic morphology

European spruce bark beetle (hereinafter referred to as bark beetle) is a medium size bark beetle. Adult and mature individuals are 4.5 – 5.5 mm long and about 1.9 mm wide (Kindlmann, 2012). Immediately after imaginal ecdysis, the colour of imagoes is white. Later, the colour gradually changes into yellow, light brown, and finally dark brown, or black. Body of beetles is shiny and covered with yellowish hair (Skuhravý, 2002). Oval eggs are white and shiny. Their size varies between 0.6 and 0.9 mm. Legless larvae are more or less white. Their size after hatching is about 1 mm. The larval development includes three instars. At the end of the third instar, the larvae are about 5 – 7 mm long (Zumr, 1995). The pupa is of the same size and colour as larva (see Figure 6 and 7).

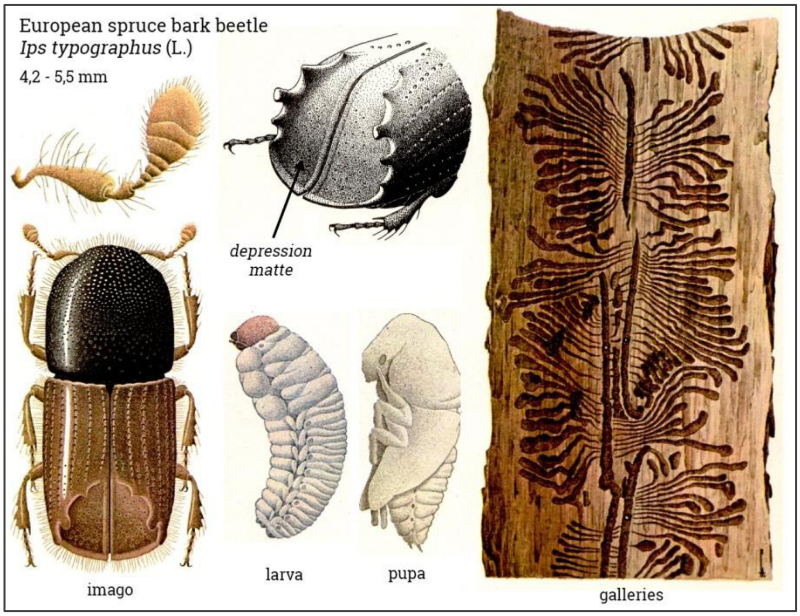

Figure 6 and 7: European spruce bark beetle. Left image taken from Novák et al. (1974) and translated/modified. Right image taken by Josef Dvořák (© Biolib, 2016).

Description: Three main developmental stages of bark beetle – larva, pupa and imago are shown in the left picture. Picture also contains main identification signs – abdomen with characteristic matte depression, a leg and an example of galleries with pattern characteristic for given species.

2.2.3.2 Life cycle and development

Except a short hosts seeking/dispersion phase, all bark beetles in broader sense share the cryptical way of life (Rudinsky, 1962). Their life cycle can be roughly divided into three phases: colonization, development and dispersion (Raffa & Berryman, 1987; Rudinsky, 1962). In case of bark beetle, the life cycle begins in spring when majority of imagoes that overwintered under the bark or in soil litter disperse to find suitable hosts. After the selection of suitable tree, males bore under the bark and excavate mating chambers which they subsequently use for mating purposes (Skuhravý, 2002).

Bark beetles are an example of polygamous species – each male mate with usually two or three females, although this can be affected by the propagation phase (Wermelinger, 2004). The sex ratio during endemic phase is about 1:1 but deviates during the epidemic phase (Skuhravý, 2002). According to Lobinger & Skatulla (1996), the population is dominated by females at the beginning of gradation (increase up to 72 %), while males prevail at the end. Anyway, when fertilized, females excavate egg galleries running parallel with the trunk axis in which they deposit up to 80 eggs placed in niches along the margins (Wermelinger, 2004). The length of the galleries depends on the tree occupancy and is negatively correlated with total density of the bark beetle population (Lukášová et al., 2004). When finished, females remain under the bark and regenerate while feeding. Later they may leave and establish a new one or even more sister broods either on the same or another tree (Wermelinger & Seifert, 1999).

The larvae feed on the secondary phloem at right angles to egg galleries thus forming the larval chambers. Each of these chambers is later ended by pupal chamber in which the larvae pupate (Skuhravý, 2002). Before new generation of beetles matures and leaves the brood trees, they spend some time in pupal chambers by enlarging them by maturation feeding (Wermelinger & Seifert, 1998).

Effect of temperature

All the life phases and especially the development of bark beetle are highly temperature dependent (e.g. Raffa et al., 2015). According to Wermelinger and Seifert, average lower temperature threshold for all developmental stages is about 8.3° C while the optimum is near 30° C. They also counted that accumulated sum of 334 degree-days is necessary for development from egg to pupa, whereas 229 degree-days are necessary for subsequent maturation feeding (Wermelinger et Seifert, 1998; 1999). On the other hand, the data slightly vary depending on different authors. For example, Wermelinger (2004) notes that data published by Abgrall & Juvy (1993) indicate that the accumulated sum required for development is higher – about 365 degree days.

Anyway, this developmental dependence on temperature results in formation of populations with univoltine or multivoltine character throughout the year. Because the number of generations is dependent on the length of vegetation season or the sum of temperatures respectively, it is indirectly dependent on the latitude and altitude of the specific area (e.g. Annila, 1969).

2.2.3.3 Population dynamics

It is typical for the bark beetle populations they exhibit facultative attack patterns. Generally, they alternate two different phases of development. For most of the time they remain in the endemic phase (Kindlmann et al., 2012). While in this phase, bark beetles act like typical R-strategists when attacking weakened or dying trees that, from the ecological point of view, represent scattered and short-lived resources (Wermelinger, 2004).

On the other hand, bark beetle populations can relatively quickly switch to epidemic phases and rapidly grow in numbers. After they reach certain thresholds they become capable of attacking and killing even vital trees which opens a whole new niche to them. This niche is rich in nutrients and relatively free from interspecific competition (Schlyter & Anderbrant, 1993). The transition from endemic (latent) to the epidemic (gradation) phase is catalyzed by the natural disturbances (i.e. droughts, heat waves or wind storms) summarizes Wermelinger (2004).

Dynamics on example of Bohemian Forest

The natural population dynamics without human intervention can be well demonstrated on example of Bohemian Forest (both the Bavarian and the Czech side) during 1983 – 2001. Because the propagation started in Bavaria and preceded the Czech part which is addressed in this thesis, description of situation in Bavaria during 1983 – 1991 as provided by Skuhravý based on the sources mentioned herein (2002) follows…

On the 1st August 1983 a strong windstorm caused a windthrow on area of 173 ha located in the Bavarian Forest National Park. Area of 88 ha was left without any intervention due to national park policy. This happened during unusually hot summer, when the temperatures measured exceeded even 32° C. Also next year another windstorm followed by a windthrow occurred. Conditions in years 1983 and 1984 favorable in terms of easily available food resources as well as convenient weather resulted in propagation of bark beetle in disturbed stands which continued also in 1985. In 1986 however, the amount of breeding material was already insufficient and therefore the bark beetle spread into surrounding healthy forest stands.

The total area of forest disturbed by windthrows and bark beetle attacks was 381 ha in 1984. During 1985 – 1987 it was extended only a little. Then, the gradation culminated in 1988 with extension of disturbed area by 105 ha of which about 26 ha was situated in high elevations. 1989 meant additional extension by 68 ha. Later in 1990 and 1991 strong winds (named Vivan and Wiebke) resulted in windthrow disturbances on area larger than 1 100 ha (which represented 11 000 m^3 of felled wood in total). The gradation seemed to linger, however. Only 21 and 14 ha of forest were killed by bark beetle in 1990 and 1991 respectively. Despite favorable temperature conditions, the area of forest disturbed by bark beetle gradually declined from 1988.

Average temperature during period 1988 – 1991 was higher than long-term average so it corresponded to conditions in elevations 200 – 300 m lower in previous years. Moreover summers in 1988 – 1990 were characteristic by small amounts of snow and precipitation in general and therefore trees were probably stressed by irregular water supply. While the population in 1990 had bivoltine character, cold spring in 1991 resulted in univoltine population. Significant decline of bark beetle population led observers to think that the gradation was in 1991 at its end but they were totally wrong.

The gradation took second breath and came back in second phase (1992 - 2001). At this time, both sides of the national border were affected and even much stronger. The total area disturbed at Bavarian side in period 1983 – 1991 was roughly 600 ha (about 1 700 ha including windthrows in 1990 and 1991), while in period 1992 – 2001 it was more than 3 600 ha (which represented about 1.5 – 1.7 million m^3 of felled wood). More than 90 % of montane spruce forest in high elevations (i.e. in the border area at Bavarian side) was disturbed during these two periods.

Main exogenous factors that positively affected the beginning and course of the population gradation were clearly as follows: strong windstorms that resulted in large windthrows that meant a sufficient amount of breeding material; at least in some years favourable conditions in terms of high temperature and low precipitation; bad health condition of the forest mainly due to high imissions in past decades; and last but not least the decision of national park authorities to not intervene.

2.2.3.4 Flight, migration and dispersion

The bark beetle is clearly a considerably mobile species (Skuhravý, 2002). Numerous studies conducted in last decades show the whole variety of bark beetle flight behavior and complex patterns of its migration and dispersion (e.g. Bayers, 2000, Weslien & Lindelöw, 1989, Zumr, 1991). It is also clear that patterns of the bark beetle's behavior are driven by both, endogenous and exogenous factors (Skuhravý, 2002).

Direction

In theoretic situation when the bark beetle wouldn't be affected by pheromones (or some other environmental factors) it would disperse equally (Botterweg, 1982). This pattern, however, is in reality altered by various factors. One of the most important factors is the wind which in fact is an example of "double-edged" force because it can function as both – the promoting as well as the opposing force. Skuhravý (2002) summarizes that if the wind speed exceeds 1 m/s the beetles tend to fly in the same direction as the wind but when the wind blows slower, the majority of them flies in opposite way. This is probably because the wind carries the olphactory signals (i.e. pheromones) at the same time.

Another very important factor affecting the direction of the bark beetle flight are pheromones and other odours captured by the olfactory system of the bark beetle within the process of so called primary and secondary attraction (Hietz et al., 2005; Blomquist et al., 2010). The colonization strategy of the bark beetle is based on joint attack of many beetles on a single suitable host so they have to have mechanisms for the localization of the right potential host as well as other beetles (e.g. Raffa, 1987).

Distance

When the bark beetle resumes its activity and gets out from the soil litter or from the underneath of the bark, it is immediately sensitive to olphactory signals and capable of the flight (Skuhravý, 2002). Generally, the intensity of the flight correlates with the temperature. The minimum temperature threshold for the flight is 16.5° C while the optimum is between 22 – 26° C, according to Wermelinger (2004).

During the initiation spring flight, the beetles can spread up to 750 m far from their overwintering localities in a single day (Botterweg, 1982). The actual length of their flight is, however, influenced by many factors – the land cover, for instance. Botterweg (1982) also reports that when the beetle is outside of the forested area, it can fly even up to 8 km distance. This is in accordance with statements of Skuhravý (2002) who logically assumes that present suitable hosts may lure the migrating beetles. The fact that the length of the flight depends on many variables is evident from different results reported sometimes even by the same authors. For example, Zumr (1991) found the maximum abundance of released beetles in the distance 1 000 m, while in another experiment he reports 300 m.

In general, the re-emerged parental beetles (who try to find a suitable host for establishment of a sister brood) seem to travel less far, according to Zolubas & Byers (1995). In contrast Fruta et al. (1996) who researched the bivoltine populations of *Ips typographus* f. *japonicus* report that individuals from the second generation disperse more extensively.

Number of beetles

The distance itself, however, isn’t informative enough because whether the attack will be successful or not depends substantially on the number of attackers. Weslien & Lindelöw (1989) report they recaptured about 13 % of beetles in relative neighbourhood of the place where they released the beetles while only 4 % of the beetles were recaptured at longer distances. Wermelinger (2004) sums that although the normal active flight distance is under 500 m, more than 90 % of successful attacks occur under epidemic conditions at the distance under 100 m from the nearest infestation source.

2.2.3.5 Host colonisation and its defence

Bark beetles are able to successfully colonize the host only when attacking more or less at the same time in relatively high numbers (Skuhravý, 2002). Yet the mechanisms of primary attraction and host selection are far from fully understood (Wermelinger, 2004). Many biotic (mainly gustatory at close ranges and visual cues at medium ranges) as well as abiotic (insolation) factors are involved in primary attraction (e.g. Andersson et al., 2009; Hietz et al., 2005; Skuhravý, 2002). It is widely accepted that the pioneer beetles attract other beetles via aggregation pheromones released with their frass. This is called secondary attraction and is actually much stronger than primary attraction (e.g. Borden & Stokkink, 1971).

Constitutive defence

Secondary phloem of conifers is rich in organic nutrients and therefore it is subjected to interest of many different groups of species from fungi and bacteria to insect and even vertebrates (Franceschi et al., 2005). This has led conifers to development of several potent constitutive as well as inducible defences against herbivores. First line of defence is represented by non-specific mechanical and chemical features that aim to prevent the penetration of the bark. The periderm serves as a mechanical barrier due to its content of lignified and suberized dead cells as well as oxalate crystals. At the same time they contain a significant amount of phenols (Franceschi et al., 2005). Research of Rosner & Führer (2002) indicates that bark beetle could enter the secondary phloem actually through lenticels to avoid this barrier.

Anyway, most of the defence mechanisms are located in the secondary phloem itself. Present lignified sclerenchyma cells and calcium oxalate crystals represent a mechanical barrier, while polyphenolic parenchyma cells are an example of chemical defence (Hudgins & Franceschi, 2004). Furthermore, the Norway spruce contains numerous resin ducts and resin blisters surrounded by resin cells. These resin cells synthetize resins rich in terpenoids that are released into extracellular lumens. It is well known, that some of these terpenoids, especially monoterpenes, are toxic to all life stages of bark beetle (Raffa & Berryman, 1987). When the bark is wounded, the raisins pressured in lumens are released and trap or push out the intruder (e.g. Rosner & Hannrup, 2004; Nagy et al., 2000). Clearly, the pioneer beetles (males) that initiate the colonization of new trees are at high risk.

Another level of defence is represented by inducible structural mechanisms. These mechanisms enable the tree to repair a damaged tissue or simply to isolate the hostile insect based on both, the controlled cell death and formation of the callus tissue heavily lignified and suberized. The wound periderm usually forms around the injuries caused by the bark beetle and limits the nutrient flow.

Chemical defence

Most important are, however, the means of chemical defence. This can be basically divided between protein and non-protein compounds. The protein-based compounds typically represented by various enzymes can promote lignification of the tree as well as directly decrease the efficiency of the bark beetle's digestion (Franceschi et al., 2005). In general, the protein-based compounds are much more specific than the non-protein ones. These (e.g. phenolic, terpenoid or alkaloid compounds) in return, are effective against broader spectrum of organisms and can be produced much faster (Franceschi et al., 2005). The constitutive resin ducts mention above can be also accompanied by additional traumatic ducts that can be even more toxic or cause additional synergic effects (Nagy et al., 2000).

In general, such complexity of defensive mechanisms may be a significant obstacle in evolving of resistances and countermeasures of the intruders (Langenheim, 1994). On the other hand,

2.2.3.6 Population density and competition

Once the host defence is overwhelmed, the advantage of high numbers suddenly becomes a disadvantage. High colonisation densities may result in high intraspecific competition among both, the imagoes as well as the larvae (Anderbrant et al., 1985). Therefore, the colonisation density is crucial for the individual fitness and the whole population dynamics (Schlyter & Anderbrandt, 1993).

Intraspecific competition

In general, there are two ways in which the individuals of one species can compete – exploitation and interference. The first type of competition occurs indirectly in case of limited resources. Basically, it occurs when the fitness of an individual is decreased due to unavailability of the resource caused by another individual. In contrast, the second type of competition occurs directly – typically, when the necessary life space (i.e. the reproduction interference) of two individuals overlaps.

It is typical for bark beetle populations with high densities that both types of competition occur together. Because the larvae compete mainly for food and space, they are mainly subjected to exploitation while on the contrary imagoes are mainly subjected to interference competition. Specifically they interfere when searching for the suitable place where they could penetrate through the bark or they typically compete for the mating partners (Anderbrant et al., 1985). It has been also shown, that parental beetles leave the trees sooner if the number of individuals on one tree is too high. As a result, the length of maternal galleries as well as the number of eggs laid is smaller (Komonen et al., 2011). Moreover, the offspring mortality rates are usually higher and even the cannibalism among larvae may occur (Doležal & Sehnal, 2007) when the population densities are too high.

Numerous authors have observed that the intraspecific competition significantly decreases the individual fitness which can be typically expressed by weight, size or lipid content (Anderbrant et al. 1985, Botterweg, 1982).

2.2.3.7 Diapause and overwintering

Diapause in general, is a life cycle strategy which enables the individuals to bridge conditions unfavourable for their development and reproduction. When seen from the other side, it helps the individuals to synchronise their active stage with favourable life conditions. In case of bark beetles, also synchronisation among individuals is of major importance because their colonization strategy is based on large number of attackers (Skuhravý, 2002). A concept of reproductive diapause means termination of reproductive behaviour, or the end of oviposition respectively (Košťál et al., 2011).

A transition to reproductive diapause in bark beetle is driven photo-periodically. According to Košťál et al. (2011) as well as Doležal at Sehnal (2007), bark beetles enter the reproductive diapause when the day-length shortens below 14.5 hours (i.e. in central Europe approximately in the middle of August). At this time, the beetles start to prepare for overwintering so their flying muscles are reduced at the extent of lipid resources for example (Košťál et al., 2011). Later, the diapause in broader sense (also called quiescence by some authors) is induced by decrease of day temperature that results in overall inactivity of beetles. Typically in November/December, the beetles almost completely stop all the activities including feeding (Hahn & Denlinger, 2007). They remain in this state until the temperature rises again, typically in April/May. At this time, their flying and reproducing activities relatively quickly and synchronously resume (Košťál et al., 2011).

Most of bark beetles overwinter in stage of imago. Small part of them, however, may overwinter also as pupa or even larva in the stage of the 3rd instar (Kindlmann, 2012). Their survival chances, however, are very little (Faccoli, 2002). Both ways of overwintering, in the bark as well as in the soil litter, are possible (Skuhravý, 2002 and references mentioned therein). However, various authors differ greatly in quantification of the actual "bark vs. litter" ratio. Skuhravý (2002) summarizes that the number of beetles overwintering in soil litter varies greatly from 4 to 80 % depending on the source of information. Skuhravý himself puts this inconsistency into relationship with developmental stages of given populations.

On the other side hand, Košťál et al. (2011) suggest different explanation. The difference between findings is probably caused by different behaviour of populations in different regions, according to these authors. It seems that most of the south and central European populations overwinter under the bark of standing trees (Faccoli, 2002; Košťál et al., 2011). One way or another, all the authors more or less agree on the close distance from the brood trees in which the beetles eventually overwinter when they are in the soil litter. For example, Pfeffer (1952) as well as Zumr (1982) report most of the beetles within 1 m. Maximal distance measured by Zahradník (1996) is 2.2 m.

Questionable remains the mortality of bark beetles during overwintering. Clearly, it is critical period in bark beetle life cycle which determines future development of the population. In general, the mortality strongly depends on micro-site conditions as well as course of weather (especially temperatures) in given winter. For example, Annila (1969) found that mortality of beetles overwintering in the moss (which meant almost constant temperature around 0° C) was only 2 – 7 % while at the same sites but above the snow cover (where the temperatures occasionally dropped even under -30° C) the mortality ranged from 58 to 100 %. Faccoli (2002) reports mean number of living individuals overwintering under the bark to be decrease by 49 %. Košťál et al. (2011) found that lethal temperatures are those under -20° C but when the temperatures are higher, other conditions (especially moisture) are very important too. In general, various aspects of overwintering and diapause are still one of the least revealed areas of bark beetle biology (Wermelinger, 2004).

2.2.3.8 Natural enemies

According to the generally accepted paradigm, the population dynamics of aggressive bark beetle species appear to be primarily driven by bottom-up forces (e.g. factors affecting the host resistance etc.). On the other hand, some authors highlight the importance of top-down control mechanisms represented mainly by the natural enemies of the bark beetle – i.e. the complex of various predators and pathogens (e.g. Reeve, 1997; Lukášová & Holuša, 2012), especially in later stages of gradation (Lipták et al., 2013). Some evidences (typically obtained in controlled experiments under laboratory conditions) support such opinions, although it is clear that they have only a limited corresponding value (Lukášová & Holuša, 2012). Still, they are interesting especially regarding the efforts to fight with the bark beetle in commercial forests or even protected forests where the intervention is appropriate but any forms of chemicals are excluded.

Predators

In general, populations of predators are connected with populations of bark beetles and their importance grows with increasing numbers of their pray (Lipták, 2013). One of the major enemies of bark beetles in brother sense are clerid beetles (Coleoptera: Cleridae) – in case of the bark beetle mainly the ant beetle (*Thanasimus formicarius* L.) – see Figure 22 in Appendix. The ant beetle prays on both – the bark beetle imagoes and the larvae too (Weslien, 1994). According to Mills (1985) as well as Weslien (1994), the larvae of the ant beetle are capable of causing high levels of bark beetle brood mortality. Single ant beetle larvae can eat about 50 larvae of the bark beetle during its development (Dippel et al., 1997). Among other predators affecting bark beetle populations are: rove beetles (Staphylinidae: e.g. *Nudobia lentus*), larvae of some snakeflies (Raphidiidae) and also some true flies (e.g. Dolichopodidae: *Medetera signaticornis*). Larvae of the last example named occur in significant numbers and each of them may eat about 5 – 10 bark beetle larvae (Dippel et al., 1997). Last but not least, the three-toed woodpecker (*Picoides tridactylus*) is also considered to be an important predator of the bark beetle (Fayt et al., 2005).

Parasitoids

Unlike predators, population numbers of parasitoids remain relatively low under the epidemic conditions and don't respond so much (Hougardy & Grégoire, 2001). Moreover, there are not many important parasitoids connected with the bark beetle. Namely few representatives of Hymenoptera like wasps (e.g. Braconidae: *Coleoides bostrichorum* or Pteromalidae: *Rhopalicus tutela*), according to Hougardy & Grégoire (2001).

Pathogens

Currently, about 20 different pathogens are known to be associated with the subfamily Scolytinae. One of them is virus (*Ips typographus Entomopoxvirus*), some are protozoa (e.g. *Gregarina typographi* and *Menzbieria chalcographi*), amoebas (e.g. *Malamoeba scolyti*) or nematodes (e.g. *Parasitaphelenchus*) but most of them are enthomopathogenous fungi (*Beauveria bassiana*), according to Lipták et al., 2013 and Wegensteiner (2007). Here I would like to point out especially at the work of Landa[4] et al. (e.g. 2007) who had promising laboratory as well as field results in application of *Beauveriana bassiana* against the bark beetle. The potential of *Beauveria bassiana* has later been confirmed also by other researchers, e.g. Popa et al. (2013).

2.3 Description of the study area

The study area is located in the most southern tip of Pilsen region in cadastre of Filipova Huť – the local part of Modrava municipality on the Czech side of national border between the Czech Republic and the Federal Republic of Germany, or the Free State of Bavaria respectively (see Figure 8).

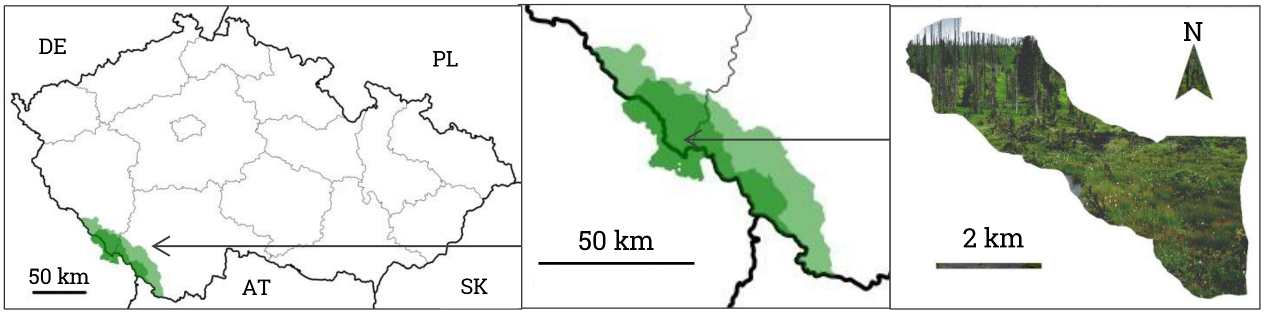

Figure 8: Localization of the study area right in the centre of the "green roof of Europe".

National border defines the study area from the eastern, southern and even the south-western side. The western border passes between local forest part called after the mountain Roklan and former gamekeeper's house of the same name. Than it

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[4] Professor Ing. Zdeněk Landa CSc. and his research team from the Faculty of Agriculture, University of South Bohemia in České Budějovice.

gradually turns to the right around the southern peak of Medvědí hora, and continuously changes into northern border. When the border meets with stream called Roklanský potok, it goes straight south against the flow where it meets an old road heading eastwards to former settlement of Březník. The border follows the road to Březník and from this point finally continues further up to the top of the mountain Malá Mokrůvka where it meets the national border again.

The whole area stretches south of the 49th parallel which goes through approximately 6 km distant Modrava village. Total size of the study area reaches 13.5 Km^2.

Figure 9: situation map of the study area.

2.3.1 Partial characteristics

2.3.1.1 Geomorphology/topography

From the geomorphological point of view the study area is located in central part of Bohemian Forest (also known as Šumava Mountains). It's a part of geomorphological district Kvildské pláně and sub-district Roklanské pláně which is the upper-most part of Šumavské pláně sub-complex. Altitude of the study area varies between 1 135 and 1 370 m with average at about 1 230 m above the see level.

It is typical for the greater part of Bohemian Forest it has a character of flat highlands with large remains of flattened surface – in other words the character of plateau or peneplain. Southern slopes fall relatively steeply down in Bavaria, whereas on the Czech side they have much more gradual tendency. The landscape here consists of flat ridges alternating with wide shallow valleys (Luzenské údolí) often filled with peat and/or moor bogs (especially moor complex of Modravské slatě which also includes the whole study area). Only occasionally some round solitary peaks (e.g. Malá and Velká Mokrůvka, Blatný vrch or Medvědí hora) protrude above the surrounding terrain. Peaks situated near the national border are intersected by the first-order watershed. All the watercourses in the study area flow to the North Sea.

2.3.1.2 Hydrology

Several major streams spring here – e.g. Luzenský potok and Březnický potok that flow together into Modravský potok further downstream. This stream together with Roklanský potok is then a major water source for the river Vydra. Except the streams mentioned above, many minor and often no-named streams also spring here. Owing to the character of the plains, all the streams exhibit only a limited erosive action which in turn helps to maintain the flat character of the study area. Local phenomenon is complemented by numerous drainless raised bogs with peat ponds and overall wet character of a large part of the study area. Since the former Roklan gamekeeper's house was built, also artificial reservoir of 1.9 ha was present at the same place. Its construction was connected with additional downstream regulations which enabled using it for logs floating (Petráš, 2010). It's not clear when and how exactly the dam was damaged[5], but for about last 50 years it doesn't serve its purpose anymore.

2.3.1.3 Climate

The whole study area is situated in cold climatic zone with transitional oceanic-continental climate. The overall conditions are very harsh – it's one of the wettest and coldest areas in the Czech Republic. In terms of local hydric regime, especially the precipitation (both vertical and horizontal) is of major importance. Thanks to presence of windward effect, the precipitation in Bohemian Forest and especially in the border area can be described as far above the average. At the same time, corresponding climadiagrams show relative balance of precipitation throughout the year. Total annual mean of precipitation measured at Březník is higher than 1 550 mm. The snow represents about 40 % of this amount and covers the study area usually for more than 200 days of the year. However, it isn't substantially involved in formation of local vegetation since it doesn't form any kinetic types.

Average annual temperature at the border area is around 2.7° C. Due to thermal inversion in Luzenské údolí and some other local depressions, however, average temperatures at the study area may be even lower. It's not an exception that night temperatures occasionally fall under 0° C even in summer months. In winter months day temperatures under -10° C are a common phenomenon. The influence of the frost as well as the wind increases at the highest altitudes. On the other hand winter inversions occur time to time and therefore the temperature at the study area may significantly rise in a short term.

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[5] It's clear that at least in 1962 the reservoir was still functional – see the aerial photo shown at Figure 10. Some sources report that the reservoir was used by soldiers from surrounding companies for water sports. It's plausible it was blown up after an accidental death of one soldier in later nineteen sixties.

Wind

The course of precipitation and temperatures aside, wind also substantially shapes local climate and ecosystems. In general Bohemian Forest belongs to one of the windiest parts of the Czech Republic. The prevailing wind direction in the whole range including the study area is from south-west. Less frequent directions are from west and south and even less frequent from other world sides. Local terrain can significantly alter the direction however, so e.g. in Luzenské údolí the south-western wind acts actually mostly like southern. Speaking about the temporal distribution, summer months are the windiest. As regards the wind power, occasional strong gusty winds or even larger gales belong inseparably to climate in Bohemian Forest and disturbance regime of local montane forests. According to Klimánek et al. (2008) there were at least six large windstorms (in 1918, 1955, 1960, 1984, 2002 and 2007) resulting in significant windthrow events in Bohemian Forest just in last 100 years.

All important and so far unquoted facts mentioned in the climate section were taken from Strnad (2003) or mined from unpublished climatic data provided by Mr. Antonín Vojvodík. Both sources are based on long term observations directly from the study area, its surroundings or less than 15 km distant 1st order meteorological station Churáňov carried out by Czech Hydrometeorological Institute (hereinafter referred as CHMI).

2.3.1.4 Geology and pedology

In a broader context, Bohemian Forest is one of the oldest and largest mountain ranges in central Europe. From the geological point of view, it belongs to Bohemian Forest group of Moldanubikum and it is composed of rocks dating from Palaeozoic and Proterozoic era. The range itself was formed by Variscan and Alpine orogeny (Kočárek, 2003; Müller et al., 1999).

The study area mostly belongs to geological unit Královský hvozd but it is also penetrated by the granulite massif of Plechý Mountain from the south-east direction. The bedrock in general is represented mainly by injected gneiss (migmatite) and granite. These are locally, typically near numerous watercourses, overlaid by sediments, eventually by peat (Müller et al., 1999, Pelc et al., 1994).

Such peaty or moor soils are common at permanently waterlogged sites. These frequently transition to peaty and peaty-humous gleys at edges of the peat bogs. At dryer parts of the study area in contrast, presence of humus podsols and cryptopodsols sporadically complemented by brown rankers is typical. Both the bedrock and the soils represent strongly acidic types (Müller et al., 1999; Neuhäuslová, 2001; Tomášek et al., 1995).

For some additional information see Materials and methods (4.2.2.1 & 4.2.2.2). Complete lists of geological substrata and soils present at the site are given in Appendix (Table 25 & 28).

2.3.1.5 Biological characteristics

All the environmental factors combined make the study area unique and valuable from the biological point of view. It's a part of broader territory which is known as the largest coherent montane spruce forest in the Czech Republic and together with forest on Bavarian side forms the largest piece of wilderness in central Europe (Kučera, 2008). At the same time, the complex of Modravské slatě is considered the largest moor complex in the Bohemian Forest.

It's not just about the alternation of spruce stands and moors – also the diversity of these ecosystems is of major significance. Although the forests and treeless areas seem uniform at the first sight (especially when inspecting aerial images), they exist in different conditions and consist of various types of communities (Neuhäuslová, 2001). The main determining force here is the local hydric regime. Each part of the study area takes the extreme form of aquatic pond, relatively dry forest or virtually anything between that. Therefore the study area is covered by a complex mosaic of different transitional phases further alternated by other conditions. Since the project is focused on forest development, the complete list of present forest communities is given in

Appendix in Table 26. Most of the present forest communities can be characterized by high degree of naturalness (for more information see Methodology – 4.2.1).

Plant species

While the whole area belongs to the 8th vegetation level according to the Forest Management Institute (hereinafter referred to as FMI) system described by Viewegh et al. (2003), way most dominant tree species is Norway spruce (*Picea Abies*). On the other hand, it's not the only one present. From time to time it's accompanied by individuals of mountain ash (*Sorbus aucuparia*) and at some places such as Luzenské údolí even silver birch (*Betula pendula*) can be found (see Appendix – Figure 23). Numerous moors and peat bogs are often overgrown by peat pine (*Pinus* x *pseudopumilio*).

The herb layer varies strongly depending on habitat specifics. Reed (*Calamagrostis* sp.) and lady-fern (*Athyrium* sp.) are typical for dryer forest stands whereas different species of cotton grasses (*Eriophorum* sp.) and sedges (*Carex* sp.) or heather (*Calluna vulgaris*) are common at waterlogged sites and peat bogs. Also European blueberry (*Vaccinium mirtillus*) is one of the major species. Generally, the wetter is the habitat, the more developed is the moss layer. Sphagnum (*Sphagnum* sp.) is here a typical representative of course but tens of other moss species are also common (another typical example is greater whipwort – *Bazania trilobatta*). Mosses are commonly accompanied by various lichens too.

Typical representatives aside, the study area offers some rare and endangered species too. The most glaring examples are: brown gentian (*Gentiana pannonica)*, felwort (*Swertia perennis*), great sundew (*Drosera rotundifolia*) or bog sedge (*Carex limosa*). In general, species diversity of present phytocenoses is very low (sum Jonášová & Prach, 2008; Matějka & Viewegh, 2011; Neuhäuslová et al., 2011; Vacek et. al., 2002).

Animal species

The umbrella species of the study area as well as the flag species of the whole national park is the western capercaillie (*Tetrao urogallus*). Relict population of capercaillie in the Bohemian Forest is the only vital population in Czech Republic (Málková et Lacina, 2002). According to monitoring carried out by the national park, the population size was estimated to be over 200 individuals in 2004 (Bufka, 2004). The study area is located in the centre of its distribution (Šumava NP, © 2008 - 2016), which is one of the reasons why non-intervention regime has been applied there and the area has been extensively closed for tourists. Taking into account also other rare bird species, e.g. three-toed woodpecker (*Picoides tridactylus*), ring ouzel (*Turdus torquatus*) or red crossbill (*Loxia curvirostra*) inhabit the area (Šantrůčková & Vrba et al., 2010).

Among big mammals red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) inhabit the study area today (Anděra & Červený, 2014) but the situation hadn't been the same all time. 150 years back into history, all Czech big predators were still present. The last brown bear (*Ursus arctos*) in the area was supposedly shot near Luzný Mountain at the border in 1875 according to unspecified Bavarian sources cited by Kothera (2005). The last wolf (*Canis lupus*) in Bohemian Forest was shot in 1891 and the last lynx (*Lynx lynx*) during the second half of the 19th century as well. The lynx, however, has been later successfully reintroduced – in nineteen seventies on Bavarian side and consequently in nineteen eighties on the Czech side (Plán péče o velké šelmy, © 2016). Current population in Bohemian Forest is more or less stable and counts about 50 individuals (Kaczensky et al., 2012). Also wolfs visit the national park time to time, although the vital population has not been established yet (Plán péče o velké šelmy, © 2016). When focused on smaller mammals, e.g. northern birch mouse (*Sicista betulina*) is one of the rare inhabitants of the study area.

The largest group of present animals are invertebrates of course. It's necessary to mention especially the unique fauna of moors and peat bogs which includes many relict species of Nordic origin. The study area abounds with various species of small crustaceans (daphnia, copepods), rotifers, larvae of various insect species (e.g. *Aeshna subarctica*), dragonflies, spiders, centipedes and butterflies (e.g. *Gonepteryx rhamni*) and others. Last but definitely not least, probably the biggest bests of all, a typical example of ecosystem engineer (Raffa et al., 2008), the bark beetle (*Ips typographus*) also lives in the local forest.

2.3.2 History of the study area

2.3.2.1 Ancient times

Thanks to the remoteness and prevailing harsh conditions, the human influence on the study area was relatively limited in distant past. On the other hand, it has begun already in prehistoric times and with increasing but varying intensity continued until presence. First people visited the area shortly after the end of last ice age – about 10 thousand years ago. They were some semi-nomadic Mesolithic tribes according to recent archaeological discoveries made by researchers from The Institute of Archaeology of the Czech Academy of Science (Čuláková et al., 2012).

It's generally believed that the first civilized people who visited the central part of Bohemian Forest were Celts, although they haven't left behind any relicts at the study area (Slabina, 2005). First material signs of human presence at the study area supposedly date back to the 9th century i.e. the Slavic era. Numerous gravel and sand piles can be found along the streams flowing from the base of Roklan Mountain and at the bottom of former Roklan reservoir. These are the remains of former highest Czech placer mining sites (Kučera, 1984; Kudrnáč, 1991).

The colonization in middle-ages was relatively slow. Human activities at the study area were limited only to occasional hunting and perhaps visiting of gold seeking prospectors. It's also known that merchants commonly used traditional trade routes passing through the area. One of them led along the border over the mountains Malá and Velká Mokrůvka. Another one went from Březník area to Špičník Mountain and further to the border crossing Modrý sloup. It's also known that people from the nearest settlements were obliged to maintain the system of border marks (Šumava - modravsko, © 2016). Anyway, the whole border area was deserted and inhospitable piece of wilderness in general. It was known under the name Královský hvozd and no permanent settlements were established at the study area or even in its broader surroundings for a long time.

2.3.2.2 Colonization from 17th to 19th century

Today, the study area belongs into cadastre of Filipova Huť which has been established as a glasswork settlement in 1785. Closer Modrava village, however, was established more than 150 years earlier – already in 1604. It should be noted that the whole settlement consisted only of about three houses at that time and it didn't grow too much until the second half of the 18th century. Numerous settlements established by woodcutters including Březník and Roklan gamekeeper's house weren't established in the area until the beginning of the 19th century.

The first of the only two settlements established in the northern part of the study area was Březník in 1804. This was directly connected with establishment of the Březník forest district which followed the acquisition of Prášily domain by the house of Schwarzenberg in 1798. At the beginning, however, the responsibilities of the local ranger based in old Březník gamekeeper's house consisted much more of game keeping rather than logging, logs floating, moors draining, or reforestation of felled forest parts. These activities were fully developed up from 1844 due to change of the management plan. Increased development of the area included also construction of a new road to Modrava and the road leading to the Roklan glade. Also new solid gamekeeper's house was built in 1856 (Petráš, 2010). The second settlement consisted of a gamekeeper's house at Roklan Glade only. None of the available sources mentions when the house was built but Petráš (2010) states it had to be sometime between 1804 and 1856. The house was accompanied by reservoir used for logs floating.

Windstorm in 1870

The windstorm in December 1868 and recurring gales in October 1870 led to one of the most severe bark beetle outbreaks of the 19th century in Europe. Windthrows occurred mainly in south-west Bohemia and adjacent regions of Bavaria and Austria. The amount of felled trees was so big, that it was impossible to process the timber on time. This caused inevitable bark beetle outbreak to start in 1872 which peaked in 1874 – 1875. During 1868 and 1870 an overall area of 9 000 ha of spruce forest was damaged. To deal with such a huge outbreak, it was necessary to summon around 7 000 local workers and lumberjacks and some more 1400 workers from abroad (Skuhravý, 2002).

2.3.2.3 Study area in 20th century

The number of inhabitants culminated at the end of the 19th century. The population of Březník settlement was 38 in 1890 but decreased to 13 in 1910. Number of inhabitants from Roklan gamekeeper's house in contrast didn't change too much. It was 12 in 1869 and only one less in 1910 according to historical sources summarized at zanikleobce.cz (© 2005 - 2015).

It's obvious that the influence of local people on the study area was not only direct as described in the previous section but also indirect. Lumberjacks were not able to transport the logs from the forest without horsepower so they had to build and maintain stables including hey management. Several heads of indispensable cattle grazed in the surroundings as well. Some of this information can be found in archive but usually undated photographs and postcards or memoirs. The most famous author commonly associated with the given place is a Czech writer Karel Klostermann. His famous novel "Ze světa lesních samot" from 1894 (1922) takes place directly at Březník settlement.

It's possible that the unprecedented popularity of Karel Klostermann significantly contributed to the increasing interest in the given area. Mainly during the time of First Czechoslovakian Republic the area became a coveted tourist destination. This is by the way recorded in preserved tourist books from both settlements. Increased tourism led in 1936 the Association of Czech Tourist to build a new mountain chalet at Roklan glade (Petráš, 2010). This building, however, didn't serve its purpose for a long time because of the upcoming World War II and military presence after the communist putsch in 1948.

Iron curtain

Just as no one knows when the former Roklan gamekeeper's house was built, it's uncertain when it was demolished as well. It probably happened at the same time when first military buildings were constructed at the area, i.e. sometime around 1950 (Petráš, 2010). These buildings served as a support for military companies dislocated at the area[6]. These soldiers, members of special forces called border guards, had virtually only one task – to guarantee the state border closure[7].

The whole system of national border surveillance especially of borders with Germany and Austria is known as so-called Iron Curtain. The system consisted of a wire fence on wooden stakes located several kilometers from the actual national border accompanied by an open area. In this case, this was provided by relatively narrow orthogonal clear-cut intersecting the whole study area. Of course also supporting buildings, roads and other facilities were present. Main examples are shown in Figures 10 and 11 below.

In 1963 the Šumava Protected Landscape Area has been established due to high natural and cultural values of Bohemian Forest as a whole (Czech Republic, 1975). The regime in the border area, however, was kind of exceptional because of the presence of border guards. On one hand the strong military presence simply had to have a disturbing effect on nature (e.g. usage of herbicides while maintaining the strategic clear-cuts) and landscape (the fence itself, clear-cuts, all the necessary infrastructure including roads and buildings) but on the other hand most of the time from most of the perspectives the border area including the study area was left completely untouched. This is especially true for the period of nineteen seventies and nineteen eighties when

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[6] Three different military companies (Roklan – located at Roklan glade, Šumná – located about one kilometer west from Březník and Březník itself) were present at the study area itself during 1949 – 1969 according to chronicles of these companies cited by Šmída (Šumava – modravsko, © 2016).

[7] This in practice actually meant shooting people who tried to escape across the border from the criminal dictatorship.

the fence system was moved further into mainland and all military activities at the study area were significantly lowered (Šumava – modravsko, © 2016).

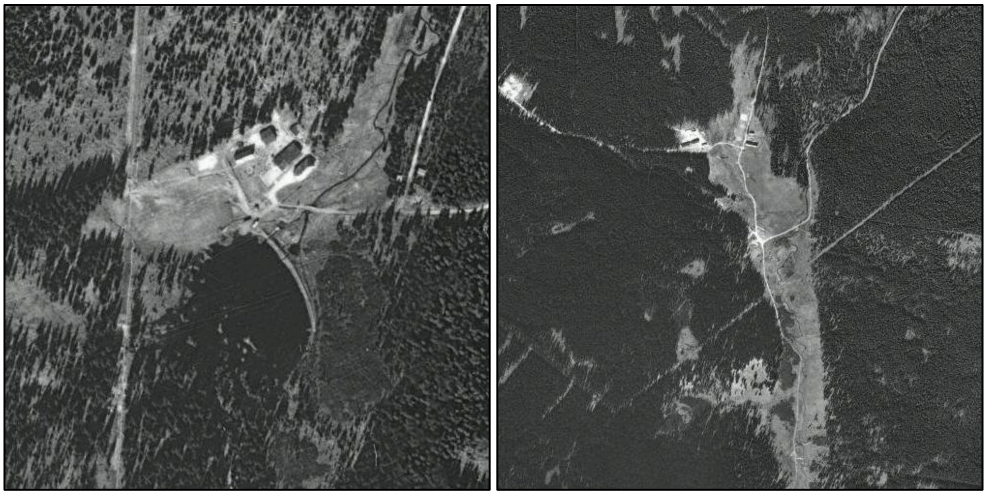

Figure 10 and 11: Archival aerial photos taken at the study area in 1962 by Military Geography and Hydrometeorology Office in Dobruška (©).

Description: Left image shows the area known as Roklan glade. Several military buildings and the Roklan reservoir were still present at this time. Right image shows broader area around Březník including a part of Luzenské údolí. Some military facilities serving the needs of border guards besides the gamekeeper's house can be distinguished at Březník. Foundations of former company Šumná are located in the north-west part of the picture. The right-angled corridor heading from the north-east to the south-west was accompanied by the fence etc. and was part of the Iron Curtain.

2.3.2.4 Nature protection era (1989 – now)

Due to its exceptional natural values, the study area together with some other parts of the landscape protected area core zone has been protected since 1989 as a natural monument Modravské slatě. Later in 1991 the central part of the landscape protected area (including Modravské slatě) was transformed into the Šumava national park (hereinafter referred to as ŠNP; CZECH REPUBLIC, 1991). At the same time, the area has a status of UNESCO Biosphere Reserve since 1990. The study area also falls under The Ramsar Convention with the name Šumavská rašeliniště since the same year

(RAMSAR, 2001). Since the join of Czech Republic to European Union in 2004 the area is on national lists of Special Protected Areas and Sites of Community Importance. Last but not least I have to mention that the core zone of ŠNP is complemented by the Bavarian Forest National Park on (hereinafter referred to as BFNP) the other side of the national border since 1970 so they constitute a compact forested area rightfully called The roof of Europe (Skuhravý, 2002).

Speaking about the national park zonation, brief and clear overview is provided by Křenová et Hruška (2012) or recently by Schneider (2015). Shortly, since 1991 the whole study area has belonged to 1st – most protected zone. Later, significant but minority part has been transferred into 2nd zone in 1995 where it has remained until today. Though it's not important in terms of the project, please note that all the serious current plans for future development suggest consolidation of the study area and the whole core zone back within 1st zone (e.g. Schneider, 2015).

Management regime

Rather than zonation, the management applied is of fundamental importance. The joint decisions of Czechoslovakian Ministers of Agriculture and Environment implied that more than 55 % of the State Nature Reserve Modravské slatě should be left under the non-intervention management regime (Dejmal, 1991; Kubát, 1991). This included the whole study area. Later the situation was changed by new decisions issued by the same ministers, which reduced the non-intervention area from 2000 to 500 – 1000 ha and ordered an immediate intervention against the bark beetle at the rest of the area (Dejmal, 1992; Kubát, 1992). These decisions, however, were applicable only for less than a week until the act no. 114/1992 Coll. came into force (Czech Republic, 1992).

Based on the decision of Minister of the Environment František Benda (Hnutí Duha, 2016) a bark beetle emergency team was established during the spring in 1993. The onset of the bark beetle spreading however was relatively slow in early nineties, so the bark beetle emergency team was disbanded later that year. The team declared that the bark beetle infestation was stopped (despite the fact that not many actions had been actually taken at the study area and virtually the whole area has been infested in later years). Since 1993, the national park administration also gained the right to define the management of forests, based on the act no. 114/1992 Coll. (Czech Republic, 1992). From that time until now the non-interventional management has been applied when it comes to salvage logging following recommendations of the ŠNP scientific board.

On the other hand e.g. in 1998 the national park administration issued a decision which granted permission to take actions against the bark beetle infestation in form of pheromone traps application and root stock clearance (Administration of ŠNP, 1998) also at the study area. Even though the expert panel of the Minister of the Environment and the national park scientific board recommended the non-interventional management regime in all the 1st zones, the national park administration announced in 1999 they will intervene against the bark beetle in selected 1st zone areas (Administration of ŠNP, 1999). This however, didn't refer to the study area anymore while the local outbreak has been almost at its end.

From the approximate historical overview[8] provided in the last section I summarize that since 1991 no significant interventions that would strongly affect the population gradation or directly caused a change of land cover were carried out at the study area during the study period.

On the other hand, it's my duty to point out that especially at the time before 1st June 1992 when the act no. 114/1992 Coll. came into force, not all the actions at the study area were taken in accordance with the national park mission or general standards of nature protection at all. For some exemplary images from the study area taken in 1991 showing the heavy machinery at work see Figure 26 and 27 in Appendix. More about the unsatisfactory situation in the national park at the beginning of nineteen nineties can be found in correspondence between local resident Zdeněk Uher and former Minister of the Environment František Benda (Mañana, © 2016). But to be completely honest, scandals don't avoid the study area even nowadays... (ŠNP, © 2014).

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[8] The legal situation was actually much more complicated and confusing but the outlines given should at least roughly correspond with the reality. This fact can be substantiated by the images from the annual aerial surveys.

3 Aims and hypotheses

3.1 Aims

This thesis has three primary aims:

1) To create a spatio-temporal model of a changing land cover at the study area during the study period (1991 – 2000) that will truly reflect the bark beetle population gradation.
2) To create a relational database consisting of environmental factors that could possibly play a role in the pattern of the bark beetle dispersion.
3) To combine the model with the database and identify the main environmental factors with the dominant influence on the infestation pattern at the stand level.

The thesis has also a secondary aim: to process the related weather data and use it for an interpretation of the infestation pattern at the landscape level.

3.2 Hypotheses

The hypotheses postulated for the purpose of this thesis are:

1) A triggering disturbance (usually a windthrow) accompanied by favorable conditions is a necessary prerequisite for onset of a bark beetle outbreak.
2) Depending on both, the population-specific factors and the habitat-forming factors, some parts of the forest are more predisposed to the successful bark beetle attack than the others.
3) The importance of the individual factors affecting the dispersion of the bark beetle significantly changes during the outbreak depending on their complex interplay in the spatio-temporal context.

4 Methodology

4.1 Land cover vectorization

The core output of my work as well as the source for derivation of numerous other data is represented by the spatio-temporal model of changing land cover at the study area during years 1991 – 2000 (except years 1992 and 1993 due to a missing data). The model primarily captures the continuous dieback of present montane spruce forests which just reflects the progressive spread and population gradation of the bark beetle.

All the data editing described in this chapter was made using the software ArcGIS 10.1[9] (hereinafter referred as ArcGIS). This program was the software of my choice dealing with most of GIS tasks during the whole project, though.

4.1.1 Remote sensing images

Information about the land cover was obtained from the aerial photos taken during the remote sensing flights carried out by BFNP during years 1991 and 1994 – 1997 and by private company Georeal Ltd. (hereinafter referred to as Georeal) on demand from ŠNP during years 1998 – 2000. Set from each year contained between 4 and 12 images of various sizes and quality. All images were provided in a digital form.

4.1.1.1 Images obtained from BFNP

The possibility to utilise annual aerial surveys carried out by BFNP since 1988 was simply given by the fact that the study area lays on the border of the both national parks, or the national border respectively. Coloured images of the national park and the surrounding area were acquired stereoscopically with an analogical camera in the

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[9] Desktop version of ArcGIS 10.1 from ESRI. This version was released in spring 2012. It was the most advanced widespread commercial GIS software available for most of the time during the project.

near infrared spectrum with the geometric resolution of 20 cm. Their spatial resolution varies between 1:10 000 and 1:15 000.

Each year involved two survey flights – the first one in June or July and the second one in September or October depending on the local conditions. I had access only to the images from the second flight but this was completely sufficient for my needs. Because of a dramatic colour change one can clearly identify the trees dying as a result of a bark beetle attack in a given year e.g. according to Lausch et al. (2013). The exact methodology of acquisition and a subsequent processing of these images before I gained them is described by Rall & Martin (2002).

4.1.1.2 Images obtained from Georeal

The images acquired by Georeal were as in the previous case taken during August or eventually later in the autumn. Therefore these are suitable for the purposes of the thesis. These are coloured images acquired in the spectre corresponding to the natural colours with the geometric resolution of 25 cm. Spatial resolution is 1:14 000. Details about the acquisition and a subsequent processing of these images unfortunately can’t be traced in any published sources due to a commercial character of the company activities.

4.1.2 Preliminary editing of the images

After examining the images I found out, that the data from years 1991 – 1999 were not georeferenced precisely enough. They contained an error that emerged probably from an imperfection of the aerial surveying and/or the subsequent processing. Common difficulties of the remote sensing and the mechanisms of errors emergence in general are described e.g. in the monography written by Barrett & Curtis (1999).

The methodological background for the procedure outlined below is described e.g. in the monography written by Schowengerdt (2007).

4.1.2.1 Rectification

For this reason, I was forced to accede to the data editing by rectification. This is one of the basic methods used for editing of raster data (not only) which works on the principle of marking the unique points in the reference image – e.g. a crossroad or the bottom of a solitary tree and their matching with an analogically placed points in the image being rectified. Since only the set of the images from the year 2000 did not contain any irregularities, I used it as a reference. Precision of this set was verified by a comparison with precise images from later years.

My workflow was as follows: first I defined a layer consisting of 60 points covering more or less equally the whole study area. These points were common for all the image sets from all the years. Then, besides the basic points, I always added some extra points with regard to the specific situation in the particular image. These additional points substituted the basic points typically when these couldn't be located due to various causes. The reason was to maintain both the equal distribution and the proportional number of the points in the image. The minimum number of the points in one image was 15. I distributed a total of 1098 points in this way (representing an average of 22.4 per image).

Georeferencing

Subsequently, the images were georeferenced based on the comparison within each pair of points using a transformation model. Specifically I chose a 3rd order polynomial model. The main condition for use of such relatively complicated model is a number of equally distributed rectification points. Various sources including ArcGis manual (ESRI, © 1995 – 2013) agree on minimum number of 10 points. This condition was met at least of 150 %. Resulting total root-mean-square error (hereinafter referred as RMS error) for the individual images ranged from 0.5 to 7.4 (3.3 on average) which I consider sufficient in terms of the purpose.

One of the inevitable consequences of the georeferencing process is the need for resampling of a newly created image. In principle, the newly created pixels of the raster have to be attributed by newly interpolated values. I chose the method of cubic convolution which calculates the value of a new pixel as a weighted average of values taken from the 16 nearest pixels.

4.1.3 Vectorization

I manually converted the information about the land cover contained in the edited raster images into vector layers for each of the investigated years. While creating the polygons I distinguished 3 different types of land cover that could be safely recognized:

- Undisturbed forest,
- Disturbed forest,
- Treeless area.

In case the images didn't cover the whole study area or the land cover couldn't be recognized (e.g. due to present clouds), I introduced also a complementary 4th category called "no data".

4.1.3.1 Vectorization rules

The first image set I converted was the one from year 2000. Later when I continued to 1999 and further into the past, I only edited the previously made layer. This approach brought me several positives. First, due to precise georeferencing the coordinates of the polygons created in the 2000 layer did not inherit any error. Second, the error in a spatial location of polygons derived in the subsequent image sets was in case of the retrospective workflow smaller than it would be when working in opposite direction. Third, vector data are more compatible with image sets acquired in later years and therefore more suitable for the possible utilization beyond the thesis.

Overlaid images

When two or more images overlaid I always obtained the information from the image with the smallest RMS error. Alternative images were used only in case the most accurate image was illegible.

No data

In contrast, sometimes the images didn't cover the whole study area or the land cover couldn't be recognized (as stated above). In order to minimize the area of such "no data" I wrote together a list of logical rules related to the possible development of the land cover in time. When applied, these rules enabled me to clarify the land cover at some of these uncertain areas and shift them into proper categories.

For example, when clouds in image from 1991 covered some parts of the forest, I examined the corresponding image from 1994. If there was an undisturbed forest, a road or a peat pond, it was clear that the same situation was there also in 1991. On the other hand, if there was a disturbed forest or a newly formed tree-less area, the situation remained unclear.

Size of the patch

The minimum size of the patch was arbitrarily set to 300 m^2 which represents exactly 1/3 of the virtual grid cell (for more information about the virtual grid see subchapter 4.4.1). Anything smaller was ignored and merged with the surrounding landscape matrix. The minimum patch size corresponds approximately to 5 trees depending on size of their crowns and local forest density. By number of 5 trees define the minimum size of the patch also other authors, e.g. employees of BFNP Lausch et al. (2011, 2013). This guarantees a mutual compatibility in case of some possible future cooperation and enables a better comparability of the results.

Vectorization accuracy

As the number of created and edited polygons was enormous (usually the order of several thousands) and the vectorization process took me many months, I had to secure the constant accuracy somehow. I achieved this by a systematic work under the constant zoom of 1:1 000.

Because of the same reason, also the occurrence of small inaccuracies in a relative position of the polygons was inevitable. These were removed using the special topological rules and layers.

4.2 Other data

While working on the theses I used ArcGIS to build a relational database for all the data acquired, processed and derived. Each year from the examined period is represented by an extra table. Attributes of these tables represent different ecological factors examined whereas each row represents a definite cell of the grid whose ID is concurrently the primary key for the whole database.

The core of the database is represented by the derived land cover data combined with the data of present geo-botanical communities. Much more data is included, however. To see the schema of the database see Table 27 in Appendix or inspect in detail the following sections.

4.2.1 Presence of various forest communities

Although the derived data of the land cover is spatially very detailed, in some respects it doesn't provide enough information. In the first place, aerial photos can't provide the information about the hydric conditions of the site in this case. However, these conditions play a key role in a differentiation of various forest communities. Even if the tree species composition and the forest structure from the bird perspective seem to be the same, actual communities may differ significantly in both the structure and the dynamics.

Because of these reasons I decided to combine the land cover data I derived from the aerial photos with a detailed map showing the present communities kindly provided by RNDr. Ivana Bufková, PhD. I could divide the general attribute "undisturbed forest community" into four additional categories with this data. The remaining two types of forest communities present at the site according to Bufková but also Neuhäuslová (2001) have been considered a treeless area. This is basically due to their irrelevance from the perspective of the project but also due to their significantly low occurrence. Other previously defined categories of the land cover, i.e. the disturbed forest and the treeless area, remained unchanged.

The vectors provided by Bufková were based on the biotope classification which was based on her field vegetation mapping. The hydric continuum looks as follows: the wettest biotopes are the transitional mires and bogs, than the peaty spruce forests, the mosaic of peaty and waterlogged spruce forests, waterlogged spruce forests, and the least wet are the "climax" spruce forests. For the complete list of the forest communities present at the given site see Table 26 (Appendix).

I decided to use the data even though they relate to the situation in 2007. I proceed from the assumption that the main differentiating driving force of these communities is their hydric regime which is not a subject to changes in such short time and therefore the communities present at the site in the nineteen-nineties should be nearly the same as in 2007.

4.2.2 Thematic maps

The database was further supplemented with information obtained from the thematic maps purchased from the Czech Geological Survey (hereinafter referred to as CGS). All the maps used had the largest scale currently available for the site, i.e. 1:50 000. Although CGS offers a total of 9 different thematic maps covering the given site, I finally used only the geological map (Pelc et al., 1994) and the soil map (Tomášek et al., 1996). This is because of various reasons including the lack of scientific foundation or the low explanatory value of the rest.

4.2.2.1 Geological map

The current geological map was first released in 1994. Later it was digitalized and now it is provided by the institute almost in the "ready to use state". It describes the geological substratum of the site by 11 unique categories. I decided to reclassify them into 9 broader categories based on their similarities (e.g. one category for two types of granite etc.). Categories "Syenite, diorite and tonalite" and "Aplite" have an insignificant occurrence and do not dominate in later years in any grid cell covering the undisturbed forest at all. Therefore I decided to exclude the grid cells dominated by these rare substrata from the final statistics. For the list of all types of geological substrata present at the given site see Table 25 (Appendix).

4.2.2.2 Soil map

The soil map which was printed in 1996 but was actually current in 1985, in contrast, had to be further processed in order to be used. That involved especially the rectification and the vectorisation. I did these routine procedures using ArcGIS. Than it provided me the information about the coverage of 5 major soil types present at the site. For the list of all types of soils present at the given site see Table 28 (Appendix).

4.2.3 Stand maps

As an important source of information about the forest structure I used the stand maps current in 1994 and elaborated by the Pilsen department of FMI. These maps have a standard scale of 1:5 000 and I got them already in the vector form. Thanks to them, the emerging database could be supplemented by the data about the age and the forest density as well as the spatial distribution of the different edaphic categories. Although the original dataset comprised of much more (e.g. number of stand levels). I finally decided not to use this data due to various (mostly technical) reasons.

4.2.3.1 Age characteristics

The age of the forest is probably the most typical example of a variable changing with time. Considering the fact that the age stated in data sources from FMI was current in 1994, I modified the data in years before and after accordingly. All the stands younger than 21 years within a given year were merged with the land cover category “treeless area”. Also another transformation followed due to serious imbalance in dataset in form of uneven representation of the individual cohorts (I can only guess whether the age was determined arbitrarily or on the basis of actual findings) and also due to a very small ecological difference corresponding to one year of the actual age difference. For these reasons I proceeded to the established forestry practise and reclassified the single years into the decades. This was also useful with regard to the later statistical processing.

4.2.3.2 Stocking density

In contrast to the age data, I was able to use the information about the forest density without proceeding to almost any editorial procedures. I assume that this characteristic remains relatively constant from the short-term perspective. Standard scale used in forest management to describe the stock density has the range from 1 (lowest density) to 10 (highest density). All categories were present at the site.

4.2.3.3 Edaphic categories

Another valuable source of the information proved to be the map of present edaphic categories. The system of the edaphic categories was developed for the purposes of the Czechoslovakian foresters and reflects especially the soil characteristics important from the economical point of view (e.g. the nutrient content, or the wetness of the site). These categories are further grouped based on the vegetation similarities into the groups representing the typical habitat conditions (Plíva, 1987). The input of the analyses was represented by the information about occurrence of 10 of these groups. For more information about the specific categories see Table 29 in Appendix XY.

4.2.4 Degree of forest naturalness

The term “naturalness” is often used but rarely defined. The term in general means the difference between the current structure and the potential natural structure of the ecosystem (in terms of age, spatial distribution and species composition) as a result of a previous direct or indirect human influence (Vrška et Hort, 2003).

The current methodology used for the purposes of Czech nature conservation, namely the management plans of specially protected areas, is incorporated in the form of an annex into the decree no. 64/2011 Coll. and has been described by Vrška et Hort (2003). Their classification system distinguishes 6 degrees of naturalness (I – natural forest, i.e. so called virgin forest; VI – non-native forest). The whole spectrum is present at the site.

My source for the data was Ing. Karel Matějka, CSc. – IDS. This is a private research company which is interested in the study area on a long-term basis. The data were generally based on the methods described above but with special attention given to the species and especially the tree composition (probably because the other characteristics are relatively disputable in mountain forests that are mainly driven by the large-scale dynamics; Svoboda & Pouska, 2008). The information about the potential natural tree composition was based on the typological map which was based on an accurate model of forest altitudinal zones published in Kindelmann (2012). The tree species composition was also adjusted according to some literal sources. I originally tried to proceed the analyses also with another dataset further “improved” by expert assessment made by Vrška himself but the results did not mean any actual improvement.. The maps were provided already in vectorised form.

4.2.5 Digital elevation model and the derived data

Several secondary datasets incorporated into the database required a proper digital elevation model (hereinafter referred to as DEM) as a substantial input for their generation process.

4.2.5.1 DEM

Various options were considered and finally the 4th generation DEM from The Czech Office for Surveying, Mapping and Cadastre (hereinafter referred to as COSMC) was purchased. It was the latest and most accurate model available for the given area at the time of the purchase. It is based on a data acquired by LIDAR[10] technology during 2009 – 2013. It's burdened by a max absolute elevation error of 0.3 m in an open area and max 1 m in a forested terrain respectively.

The DEM was obtained from COSMC in form of a regular grid (5x5 m) of discrete points with the precisely defined elevation and geographic coordinates. Necessary tasks associated with editing and adjusting of such raw data consequently had to be done so I performed those using ArcGIS. An output of this partial phase was a DEM in raster format which was suitable as an input for the following analyses.

4.2.5.2 Potential incoming solar radiation & area solar radiation

The amount of energy received in form of solar radiation substantially affects both – the spruce trees and the bark beetles too. Naturally such data don't exist for the study area so I had to accept a compromise (as same as in many other cases) and proceed to an analysis of the potential incoming solar radiation (hereinafter referred to as PISR) and the area solar radiation (hereinafter referred to as ASR). In short, the radiation values are dependent on the slope and the aspect of a given site, the latitude, the diurnal and annual sun position and the transmission through the atmosphere. Therefore an approximate data can be derived from a DEM and some additional information (Corripio, 2003).

First I did not make the analysis only in ArcGIS[11] but also in SAGA GIS 2.0.8 (hereinafter referred to as SAGA)[12] and in both cases in two versions – for the

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[10] LIDAR is commonly considered an acronym of Light Detection And Ranging (but it's actually a portmanteau of words light & radar). Anyway it's a remote sensing method (not only) of distance measuring based on illumination of the surface with laser light.

[11] The tool is called Area Solar Radiation. More can be found in ArcGis manual (ESRI, © 1995 – 2013).

“vegetation season” from May to August and for the whole year. Because the both functions differ to some extent I finally decided to incorporate them both into the database. On the other hand, I excluded the whole year versions due to the worse results achieved in the preliminary statistical analyses. The values of the outputs represent the cumulated values of watt hours per a square meter [$Wh \cdot m^{-2}$] in case of PISR and watt hours per square meter [$kWh \cdot m^{-2}$] in case of ASR. The selected procedures are principally the same as those used by Berec et al. (2013).

4.2.5.3 Heat load index

Using ArcGis[13] I also calculated another variable called Heat load index (hereinafter referred to as HLI). Although HLI is basically a similar analysis as PISR it also takes differences between slope orientations into account. In general – a southwest facing slope should have warmer temperatures than a southeast facing slope, even though the amount of the solar radiation they receive is equivalent. This was solved by McCune and Keon (2002) and later improved by McCune alone (2007) whose method “folds” the aspect adequately so the highest values are southwest and the lowest values are northeast. In addition, the method accounts for steepness of a slope which is not addressed in most other aspect rescaling equations (Evans, © 2014).

4.2.5.4 Topographic wetness index

Topographic wetness index (hereinafter referred to as TWI) is a type of state wetness index commonly used to quantify the topographic control on hydrological processes. It combines the local upslope contributing area and the slope in the calculation (Sørensen, 2006). Various kinds of the index can differ, however, usually depending on the calculation of the upslope contributing area (Qin et al., 2011). I originally tried two

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[12] SAGA is an example of alternative, free open source software suitable for many GIS applications. Specific module used in this case is called Potential Incoming Solar Radiation (SAGA-GIS, © 2010).

[13] Calculation of HLI is not standardly supported in ArcGis so I had to download the respective tool from a 3rd party. I used a freeware tool package called: ArcGIS Geomorphometry & Gradient Metrics v1.01 developed by Jim Oakleaf and Jeffrey Evans (© 2014).

different versions – one made in ArcGIS and one from SAGA. While the second one achieved better results in the preliminary analyses, I incorporated only this one into the final database.

4.2.6 So-called Kappa index (beta-version)

Kappa index[14] (hereinafter referred to as KI) is my brainchild although it could never be invented without the background provided by both, my supervisors and the related work of other researchers worldwide. The limited mathematical apparatus has been unofficially discussed and opposed by Ing. Petr Kadaňka[15]. The future improvements are expected while it is still a beta-version.

4.2.6.1 Basic information – what is KI?

KI is basically a meta-variable that serves as a predictor of the bark beetle infestation based on the exact pattern of the infestation in the previous year. In other words it represents the probability that some part of the undisturbed forest will be successfully attacked by the bark beetle in the given year deduced purely on the spatial distribution of the sources that emerged in the near surroundings in the previous year.

The concept of the index builds on the three main assumptions:

1) Current bark beetle colonization is directly dependent on a nearby infestation source(s) from a previous year. Without the driving force – there is simply no disturbance.

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[14] The name has a dual character. First it refers to letter "kappa" from Greek alphabet which is used to record the sound "k". Yet, this is a first letter of word bark-beetle translated into Czech (kůrovec). Second, it's a hidden reference to a mythological Japanese beast „Gappa" (Daikyojū Gappa). Interpretation depends on the reader...

[15] Ing. Petr Kadaňka. Contact: nestaron@centrum.cz.

2) Each source can be described by just a few key variables – namely: an area of the patch (which is more or less proportional to the number of beetles it holds), a distance to a potential host and a direction to this host.
3) All these variables are bound together and simply can't be separated. If that happens, they no longer describe the reality in a complex way.

The facts named in points 1 and 2 and the specific variables named in point 2 are nothing new to authors dealing with the modelling of the bark beetle infestations (among others e.g., Kautz et al., 2011; Lausch et al., 2011). The problem is all these authors usually try to explain the infestation pattern using the individual variables instead of combining them into one complex meta-variable. KI is nothing more or less than this.

4.2.6.2 Key variables

All the variables had to be obtained from spatial analyses of the infestation pattern (in my case – it was done in ArcGis and I naturally used my model described above. The analyses were performed in the buffer zone of 100 m which was further extended to 200 m in case of sources from 1991 due to a lack of data from 1992 and 1993 – that fully corresponds with the mask criteria described below. For more information see subchapter 4.4.1.

Area of source patch

The area of an infestation patch is of a major importance while it represents information about the potential strength of the source. Generally – the larger the patch is, the more infested trees it contains, the more beetles will fly from it next year and the higher is the probability these beetles will successfully colonize new trees (e.g. Skuhravý, 2002). On the other hand, it is only a potential. As I assumed above, the variables are strongly connected and it depends on the others – mainly the distance, whether the potential will be fulfilled or not. Due to an occurrence of some very small source patches I decided to exclude these from the analyses – the limit for minimum patch area was set to 100 m^2.

Distance to potential host

Distance between the source and a potential host is of significant importance because of several reasons. Although chemical signals of both the beetles and the trees alternate the pattern of the dispersion to some extent, we can simply assume that the density of beetles decreases with an increasing distance because they are dispersed on larger area (Bayers, 2000). Analyses of infestation patterns at the study area suggest that the possibility of a successful attack is relatively high at the close distance whereas from certain point it more or less gradually decreases at the longer distances almost up to the zero chance for a successful attack. Therefore not only the area of each source patch detected in 100 m buffer zone around the patches of undisturbed forest was measured but also their distance.

Direction to potential host

The dispersion and the actual flight of beetles can be significantly alternated by some environmental conditions. It is probably not as important as the two previously mentioned variables but still significant. Among others, wind stands out thanks to its nature – it acts in terms of directions too. As a significant force it can possibly support or counteract the dispersion, therefore not only the area and the distance of the source but also its relative position to the potential host is relevant. First I considered several ways of a direction classification but finally I chose the simplest system of four main world sides with just one modification. The direction categories in my concept are shifted by -22.5° so one of them favours the wind direction prevailing at the study site and the main directions (e.g. 0°, 90°, etc.) were not on the edge of the sector[16].

For more information about the wind conditions at the study site see Review (2.3.1.3) or Discussion (6.2.3.1).

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[16] This fact was important due to a way how the actual ArcGis function I used determines the angles. I admit this method wasn't probably the best solution and this part of KI deserves some revision.

4.2.6.3 Some additional KI background

Considering the nature of the given factors and the complexity of their combination I was not able to express the colonization pattern by a single equation. Therefore I grouped the individual patches based on the combination of their variable classes and then assigned different equation for each of these groups separately. While defining the classes I came from the following assumptions:

1) The potential strength of a bark beetle attack is directly proportional to the area of the source.
2) The probability of a successful attack is indirectly proportional to the distance between the source and the potential host. The highest probability of successful attack is in the adjacent areas and the nearest neighbourhood of the source. At longer distances (more than 5 m) the probability decreases which can be best expressed with the logarithmic function.
3) Considering the prevailing wind direction and its strength, the best conditions for the dispersion should be in the north-east direction.

It is important to note that the basic premise was to treat each individual source separately due to its own unique combination of variables. The sum (the actual KI) of the partial values (just κ) related to undisturbed forest in one cell had to be counted just finally at the very end.

Equations

The core equation derived from the infestation pattern analyses based on data from the study area and most of the study period (1996 - 1999)[17] was as follows:

$$\mathrm{K} = V(Aa \ln d + b)$$

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[17] Data from year 1991 end 1994 couldn't be used due to discontinuity in data. Infestation pattern in 1995 was kind of exceptional and I decided to exclude it from these analyses. Year 2000 didn't provide me enough data.

...where A stands for area, d for distance and the coefficients are $a = -2.7$ and $b = 12.55$. $V = 1$ when the potential host is located in the direction between 67.5° and 157.5°, whereas $V = 0.85$ in all other cases. This equation was used to calculate the K value in case the distance between the infestation patch and the potential host was between 5 and 100 m.

In case the potential host was adjacent to the infestation patch or at a distance smaller than 5 m, the equation was as simple as follows:

$$\mathrm{K} = 50VA$$

By using these equations I was able to determine the partial values of each individual infestation patch (larger than $100\mathrm{m}^2$) at the study area. Determining KI for the patches of the undisturbed forest was therefore only the question of making the sum of the values related to them, i.e. located in the 100 m buffer zone. The respective equation was:

$$KI = \sum_n \mathrm{K}_n$$

Some key results on which the equations have been based are presented in Results 5.3.1 .For a practical example of the KI determination in action see Figure 12.

4.2.7 Wetness index

As a factor potentially representing the health condition of the forest I used the Brightness and Wetness components of Tasseled Cap linear transformation obtained from the Landsat TM/ETM+ scenes (Crist & Cicone, 1984; Kauth & Thomas, 1976), which has been shown as the most appropriate remote sensing indices to describe the insect forest disturbance (Skakun et all, 2003, Wulder et al., 2004; Jin & Sader, 2005). To obtain the trend of both indices, the linear regression was calculated from the indices values from year 1984 to one year before to bark beetle attack for each 30 x 30 m cell. As the actual predictor of a bark beetle attack I used use the slope of the regression.

4.3 Weather data

All the weather data used in the following chapters were acquired from CHMI.

4.3.1 Temperature

The data concerning the temperature were automatically measured at the climatic station in Luzenské údolí directly at the study area. The values were later manually transcribed in form of so-called Mannheim[18], mean and min/max temperatures by CHMI.

4.3.1.1 Mean temperatures

The calculation of the mean values for the individual days was based on the Mannheim temperatures using the standard equation:

$$T_{mean} = (T_7 + T_{14} + 2T_{21}) \div 4$$

These values were consequently used for a calculation of the mean temperature for the individual months and years.

4.3.1.2 Degree days

In general, it is considered to be a common problem that the mean values are not representative enough for the temperature based models of insect development (e.g. Baier et al., 2007). For example, in case of the bark beetle, the development threshold is at about 8.3° C. If I used the mean temperature, I would consider each day with the

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[18] So-called Manheim temperatures are a common standard used also by CHMI. It basically consists of three values – temperature measured at 7:00, 14:00 and 21:00.

mean temperature below 8.3° C as non-productive. At some part of the day, however, the actual temperature might be even far above the threshold so the bark beetle could theoretically significantly progress in his development. A commonly applied solution for this problem is the concept of so-called (cumulated) degree days.

The degree days are a common method used for modelling of a plant or insect development (e.g. Caicedo, 2012). Regarding the bark beetle models it is included e.g. in the PHENIPS phenology model developed by Baier et al. (2007). Basically, the method works with the assumptions that the development of the given organism is limited by a lower and upper temperature threshold, whereas the organism needs a certain total amount of heat to develop from one point to another. This amount is represented by the degree days. One degree day is equal to a one day period with constant temperature of 1° C or a half day period with temperature of 2° C respectively etc. The whole concept is described in detail e.g. in (Day, 2006).

Calculation

As implies from the information stated above, the knowledge of the course of the temperature during the day is necessary for the successful calculation of the degree days. While I did not have such information, I had to accede to the approximation using some mathematical function. This approach is relatively common and is based on the fact that the fluctuation of temperature between its minimum and maximum depends mainly on the basic physical laws (Day, 2006). I personally decided to approximate the temperature curve with a double sine function which was first introduced by Allen (1976). The calculations were proceeded in an on-line calculator powered by the University of Carolina – the department of Agricultural and Natural Resources (© 2014). The lower threshold was set up to 8.3° C. The option of an upper threshold was omitted due to its irrelevance under the conditions at the study area.

4.3.2 Precipitation & snow

The precipitation was measured directly at the study area using an automatic totalizator (see Figure 21 in Appendix). The cumulated values of six months were later converted for the individual months and calibrated by data from the surrounding climatic stations by CHMI. The data about the length of the snow cover as well as the thickness of its layer was measured manually at several sites of the study area by CHMI (Vojvodík, 2016 in litt.) once per few days depending on local conditions.

4.4 Statistical methods

4.4.1 General statistical approach

The basic idea of the statistical analysis was based on conversion of the observed reality into the statistical units. Therefore I superimposed the study area by a grid which notionally divided it into several tens of thousands of cells with an equal size but different spatial coordinates. These identical cells were of square shape and dimensions of 30 x 30 m (i.e. 900 m^2 large). Their arrangement was chosen so they were fully compatible with Landsat TM/ETM+ scenes. This was also the reason why I did not choose to work under the national S-JTSK East North coordinate system but chose the international WGS-84 UTM 33N instead.

Subsequently, each cell was described by the information about each investigated factor spatially corresponding to the respective part of the study area. This step resulted into a creation of a database used for some preliminary analyses designated for exclusion of the redundant versions of some factors (e.g. ArcGIS version of TWI etc.). By this exclusion I came to the final form of the database used in the construction of the GLM models. Similar approach but with certain differences and different statistics was used e.g. by Lausch et al. (2011). The design of the final database is presented in Table 27 (in Appendix).

Although all the factors were finally transferred to the grid which resulted in a formal unification of the spatial resolution, I did not reconcile with the loss of some information in case of spatially accurate data. This is why I acceded to the relatively time consuming extraction of the data related just to the relevant part of each cell spatially corresponding with the undisturbed forest. Application of this procedure actually does not have any literature backing – I decided to use it just based on my logical reasoning. For the representative example of the whole approach in action see Figure 12 below.

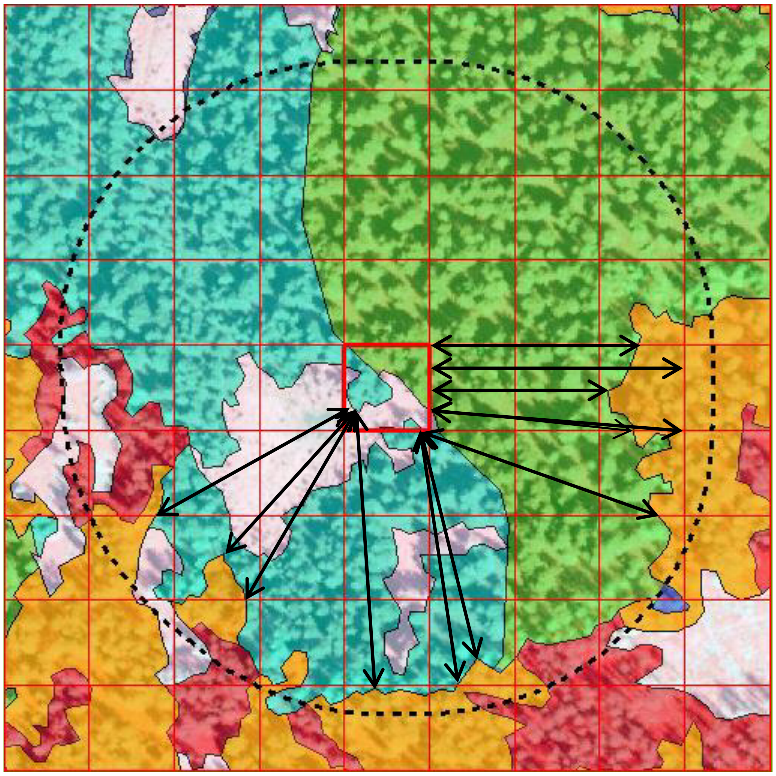

Figure 12: example – map of land cover in 1996 around the grid cell no. 42 919.

Description: this representative screenshot captures an area of 9x9 grid cells covering a no-name peat bog and its surroundings (the same peat bog has been used also as an example in Table 1 and 2 in Results). The situation is from 1996 so it would be used to interpret/predict the situation in 1997. The coloured patches represent: white – treeless area, pink – disturbed forest (1991 - 1994), orange – infestations from the previous year (1995), green – "climax" spruce forest, cyan – mosaic of waterlogged and peaty spruce forests, blue – waterlogged spruce forest, purple – peaty spruce forest (last two types are present only on very limited area).

The following description is related only to the cell in the middle of the picture which is highlighted by the bold frame. Typical procedure would be: 1) verification of the validity for the statistical analysis, i.e. measuring the distance to the nearest infestation patch from the last year (has to be < 100 m) and measuring the area of all the undisturbed forest within the cell (has to be > 300 m^2). 2) Determining whether a significant disturbance (> 300 m^2) occurred within the cell in the next year – i.e. determining the mask. 3) Creating a 100m buffer around the patches of undisturbed forest present in the cell (dashed line). 4) Measuring the area of all patches (> 100 m^2) of forest disturbed in the previous year intersected by the grid, the nearest distance (arrows) between them and the patch of undisturbed forest in the cell including the measurement of geometric angle between the connector and hypothetical line at angle 0° - everything within the buffer created in the previous point. 6) Counting the κ for each of the disturbance patches and consequently combining these partial values into final KI value. 7) Assigning the values of factors counted only for the whole cells (i.e. so-called static factors – e.g. elevation from DEM, ASR/PISR, Wetness Index etc.). 8) Assigning the values of so-called dynamic factors based on the intersection of their layers with layer of undisturbed forest (i.e. values corresponding to treeless area or disturbed forest within the cell are ignored) – e.g. geological substrata, age class, edafic categories etc. 9) Putting everything all together and thereby creating a new row in database (with number 42 919). 10) Deriving some secondary categorical factors – e.g. Wet, Land etc.

4.4.1.1 Mask

One of the problems connected with modelling of the bark beetle infestation probability is the fact that when the infestation is not observed it doesn’t have to mean that the given part of the forest was not suitable for the attack or that it was suitable but the trees have successfully defended. It can actually mean that there were simply no infestation sources in the near surroundings, e.g. according to Kautz et al. (2011).

To prevent this situation I created a mask which evaluated all the grid cells in the given year and classified them into two basic groups – the cells that could be possibly attacked and the cells that did not meet the basic conditions for a future occurrence of the disturbance. These conditions were:

1) At least 1/3 of the cell covered by the undisturbed forest,

2) The maximum distance of the undisturbed forest within the cell to the nearest potential infestation source from the previous year max 100 m.

After I divided all the cells into these categories I worked only with the potentially disturbable cells. I further divided them into another two categories – those disturbed in the next year and those not disturbed. Thus the generated mask represented a binary response variable I used in later statistical analyses. While the number of disturbed and undisturbed cells was never the same I always reduced the larger group by a random selection to the exact size of the smaller group.

4.4.2 Generalized linear models

The database of all the environmental factors described above (except the weather data) was used in the statistical analyses to explain the actual development in the individual cells under the binary mask. I specifically decided to use the generalized linear models (hereinafter referred to as GLMs) and all the analyses performed in software R[19] 3.0.3.

Basically, GLMs are the mathematical extensions of the linear models against which they are often delimited. A significant limitation of the basic linear models is that they cannot fit the response variables that do not have a normal error distribution. Moreover the explanatory values in these models have to have a homogenous variance (homoscedascity). The problems can also arise in case of dependent data (e.g. when they are spatially or temporarily correlated) or when the leverage is too high. At least some of these assumptions, however, are not met in most of the cases in ecological modelling (including my dataset). While the second two assumptions are a problem in the basic linear models as well as in GLMs, the distributional assumptions as well as

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[19] According to the official webpage, R is simply "a free software environment for statistical computing and graphics". More can be found at the project webpage: https://www.r-project.org.

the heteroscedascity can be overcomed using GLMs. More about GLMs can be originally found in McCullagh & Nelder (1999) or e.g. in Pekár & Brabec (2009).

4.4.2.1 Distribution and link function

While my response variable (i.e. the mask: disturbed/not disturbed) has a typically dichotomous character, it is well suitable for the binomial distribution which I, therefore, used. At the end, when I had the models already, I checked the fit to the quasi-binomial distribution as a part of the over-dispersion verification process. The fit was better with the binomial distribution (the parameter of over-dispersion was roughly around 1).

When the distribution for residuals of the model was chosen I still had to choose a link function for the expected values. I decided for the standard logit link function, therefore the models represented actually a logistic regression. The background for this decision was obtained from Pekár & Brabec (2009).

4.4.2.2 Models construction

I built a model for each year from 1995 to 2000. The model for 1994 was omitted due to insufficient data necessary for characterisation of the situation in 1991 as well as the data hiatus between 1991 and 1994. The description of the procedure used in building each of the models follows.

First step after data import and some necessary editing was the creation of a reference null-model which carried the information about the variability of the response variable. Subsequently I used two different building methods – just to compare the results and check the validity of my progress. First I acceded to building the model using a stepwise forward selection method[20] where the selection was based on the Akaike information criterion (hereinafter referred to as AIC). After I started the function, the program carried out an autonomous iterative process at the end of which

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[20] The exact function in R is called step.

it suggested me a "best" model. As stated above, I used this model just for the comparison with the second model I made.

Second model was built using the method of simple forward selection[21]. I started with model with only one explanatory variable – the one which achieved the best results based on the AIC in the previous method. After that, I created an auxiliary model which consisted of all variables except the one which was added in the previous step. Based on the smallest AIC in the auxiliary model I chose the second best variable and added it into the model. Consequently I created the second auxiliary model without the two variables previously excluded and chose the third variable... I repeated this pattern as long as the variables were significant (at 0.05 level).

When all the remaining variables in the auxiliary model did not show any significant difference any more, I carried out an ANOVA and compared all the models "manually" created in a Chi-square test to get the whole image about the differences between them. I chose the last still significantly different (at 0.05 level) model and subjected it to the procedures listed below. When I had doubts about the possible correlations between two factors included in the model I also made a correlation test[22].

4.4.2.3 Predictive power and goodness-of-fit assessment

The predictive value of each model was evaluated by a comparison of its deviance with the deviance of a null-model. Using a simple equation I was able to compute a pseudo-R^2 statistic which is analogous to the coefficient of determination R^2 in an ordinary least square regression (which is a method used for basic linear models). The equation was as follows:

$$Pseudo\text{-}R^2 = \left(D_0 - D_r\right) \div D_0$$

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[21] This is also known as the method of single term additions – the exact function in R is called add1.

[22] Depending on the character of the variable I used the Pearson's chi-squared test (for continuous) or the Fisher's exact test (for categorical data).

…where D_0 means the deviance of the null-model and D_r means the deviance of the evaluated model. This procedure is described e.g. in Hosmer et al. (2013).

Another method I used for the evaluation of the predictive power of the models was the coefficient of discrimination as proposed by Tjur (2009). Basically, the coefficient represents the difference between the means of the expected probability values for the successes and the failures, so the equation is as simple as:

$$D = \overline{\pi}_1 - \overline{\pi}_0$$

…where $\overline{\pi}_1$ is the mean of expected probability values when the outcome is observed and $\overline{\pi}_0$ is the mean of expected probability values when the outcome is not observed. The closer is the D value to 1, the better is the predictive power of the model (as same as in case of *Pseudo-R*^{2}).

The basic assessment of goodness-of-fit was performed using the Hosmer-Lemeshow test. Basically, the test separates the expected values into groups of approximately equal size (I used a standard number of ten groups). After that, the test compares the number of observed outcomes with the number of expected outcomes within each group. The result of the test is represented by a p value. When p was lower than 0.05, I rejected the given model and had to find another one (a shorter one, typically) which was able to pass the test. The test is described in detail in Hosmer et al. (2013).

5. Results

5.1 Change of land cover

As described in detail in Methodology 4.1, one of the core outputs of my work is represented by the spatio-temporal model of rapidly changing land cover at the study area during years 1991 – 2000 which truly reflects the population gradation and the dispersion of the bark beetle as well as the changes regarding a treeless area. All the important observations of a land cover change including the specific areas, the ratios, the patterns etc. are presented below.

5.1.1 Treeless area

The detailed analysis of a land cover shows that a treeless area covered about 23.6 % of the study area in 1994[23]. As the forest disintegration continued, the ratio between a treeless area and a forest changed to some extent in favour of a treeless area. Actual coverage in 2000 was about 25.8 % (that means an increase of about 9.4 %).

All the treeless patches that formed during years 1992 – 2000 occupied the total area of almost 30 hectares. The major part of them originated as an extension of the existing treeless areas at the expense of previously disturbed forest. These patches represented roughly about 80 % of a newly formed treeless area not only by the number of patches but also by the area covered. The occurrence of the new treeless patches was significantly clustered at lower scales but clearly aimed to a more distributed pattern when scaled up. Graphical representation of this statement is provided in the following Figure 13. Surprisingly, the size of the largest uniform treeless area, Luzenské údolí, or selected large peat bogs, remained practically unchanged.

According to aerial photos acquired in following years, the trend of deforestation and expansion of the treeless area continued and even accelerated.

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[23] Year 1994 was used instead of 1991 due to missing data.

Dieback of present trees was followed by gradual loss of forest density and emergence of small gaps. The individual dead trees, however, often remained in upright position for many years until a new generation of spruces replaced the previous one. Therefore the whole area was never absolutely deforested.

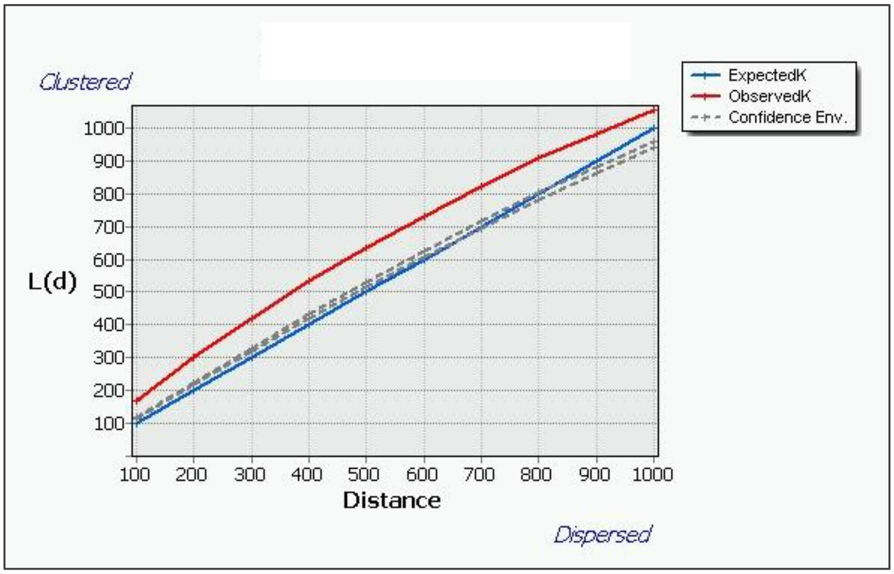

Figure 13: Distribution pattern of treeless patches formed during years 1992 – 2000 within the forested part of the study area under different scales.

Description: Distribution pattern of newly formed patches at various distances was examined in ArcGIS using the so called Ripley's K Function[24]. The observed distribution of treeless patches is represented by the red line. The distribution pattern is rather clustered when it lies above the expected distribution (blue line) and equally dispersed when it lies below it. Results are significant when the line is beyond the confidential intervals represented by dashed lines. Detailed information about these statistics can be found in sources named at the end of the relevant chapter of ArcGIS manual (ESRI, © 1995 – 2013).

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[24] I used ArcGIS tool Multi-Distance Spatial Cluster Analysis. As regards the options – edge discrepancies were treated by simulation of the outer values by addition of respective "mirror points" and the confidential envelope was constructed using nine permutations. More about the tool can be found in ArcGIS manual (ESRI, © 1995 – 2013).

5.1.2 Forested area

Total forested area declined during the examined period from 76.6 % in 1994 to 74.5 % in 2000 due to processes described above. Much more important was the quality change of the forest, though.

Dispersion of bark beetle and consequent dieback of spruce stands at the study area took about 10 years and its nature was highly progressive. At the beginning in 1991 only several small patches were present mostly in areas near the national border but most of the forest (more than 90 %) was untouched. As time passed, the initial patches gradually reproduced and grew in both size and numbers until they finally merged. Also new enclaves were established at the same time and with increasing intensity underwent similar development in consequent years. In 2000, at the end of the examined period and the gradation itself, the ratio was already turned over with about 90 % of the area disturbed.

The change of the forest cover and structure naturally continued also after the large-scale dieback of the spruce stands. Two basic processes went against each other here – the disintegration of previous tree generation and establishment of a new one. Aerial photos from later years show that large-scale disintegration of the tree layer didn't occur at least until 2010. It's obvious from both, recent field observations and aerial surveys, that falling trees gradually make space for present or newly emerging seedlings. Such released seedlings grow rapidly and in near future alternate the former generation of trees.

As a representative example of these processes in action see the Table 1 in 2 showing the change of the forest in the surroundings of a small peat bog located within the study area. This no-name peat bog is located approximately 800 m west from Luzenské údolí as the crow flies[25]. The gradual bark beetle dispersion is also presented in form of Figures 14, 15 and 16.

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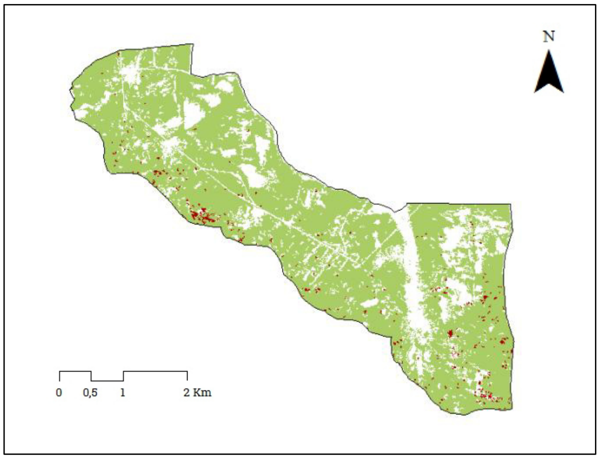
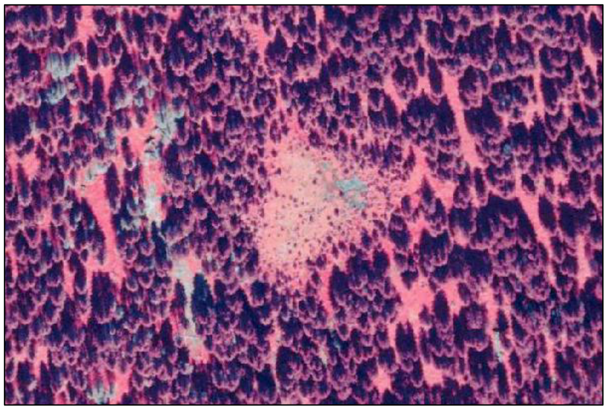
[25] GPS coordinates of the site are as follows: 48.9560953N, 13.4755969E.

5.1.3 Spatiotemporal model of forest disturbance

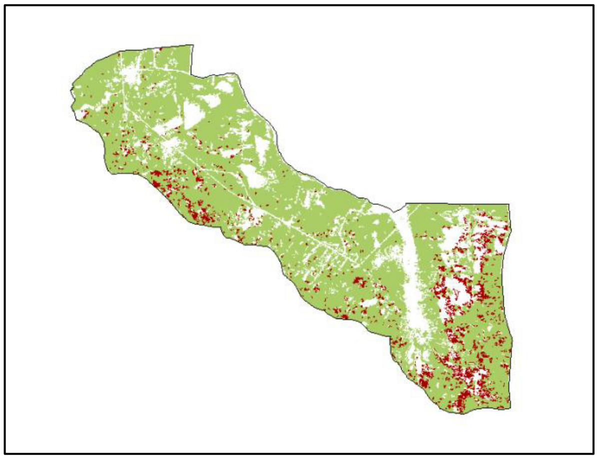
Table 1 given below shows in a two-year interval (year 1993 is exchanged by 1994 due to missing data) a cumulating area of disturbed forest. The landscape model is complemented by respective aerial images of a specific site chosen from the study area.

Table 1: Spatio-temporal model of forest disturbance at the study area during years 1991 – 2000 complemented by representative aerial photos of a small peat bog and adjacent forest.

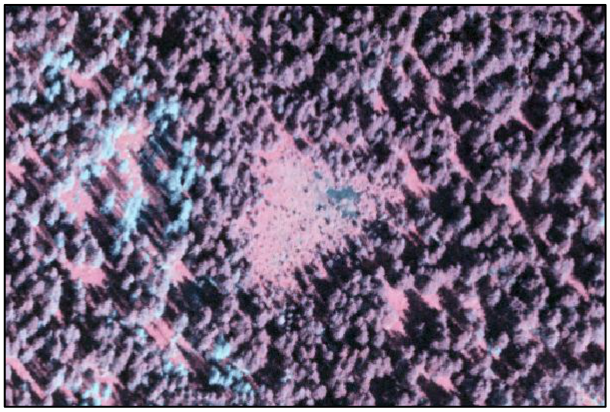
Description: Speaking about the model on the left, the light green colour represents undisturbed forests whereas the dark red colour means cumulative disturbance (i.e. forest dieback caused by the bark beetle outbreak). Regarding aerial photos on the right, first three of them were acquired in near infrared spectrum – therefore disturbed trees can be distinguished by the light blue colour. The other three images were acquired in the spectrum corresponding to natural colours so the colour of dying/dead trees is grey/brown. Each year is entitled by a dispersion phase adapted from Lausch et al. (2011). Short descriptive commentaries are given.

1991: Latent phase	
 The landscape matrix of the study area is formed by undisturbed spruce forest. Only small patches are disturbed due to colonization of bark beetle mainly in the border area.	 Small peat bog (in the centre of the image) is surrounded by undisturbed forest except the northwest part where a group of trees, for reasons yet unexplained, didn't resist the initial attack of bark beetle and died.

1994: Medium-perennial gradation I

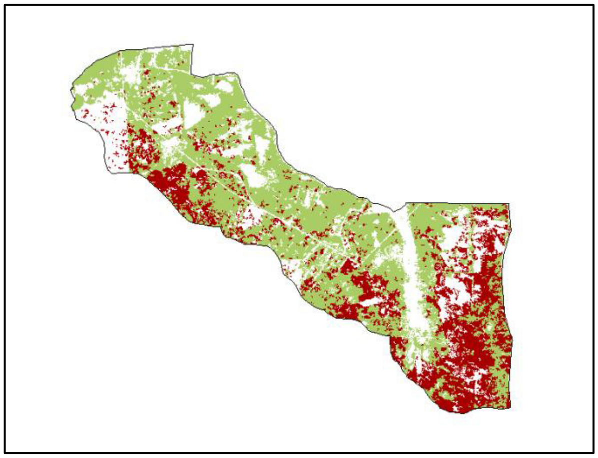


Since the conditions are favourable, bark beetle continues the dispersion to favourable areas mostly in the nearest forest (max. about 500 m from southern and 1000 m from eastern border).

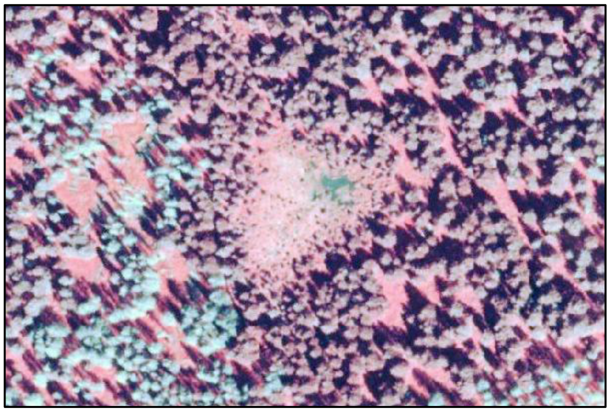


Although remote sensing methods can't reveal the true source of the infestation, it's probable that all newly infested trees were attacked mostly by bark beetles from previously established local population.

1996: Medium-perennial gradation II

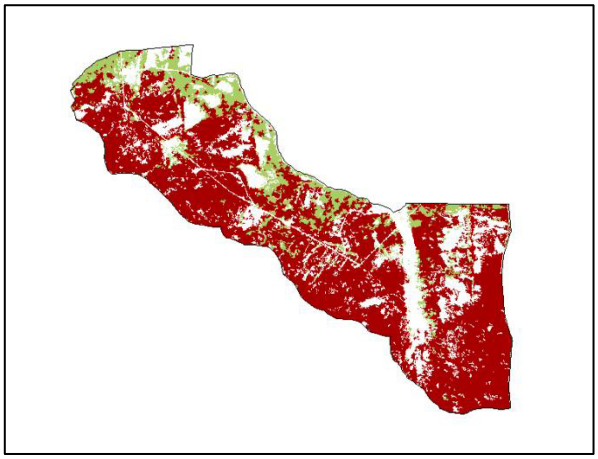


As the colonization continues, the bark beetle population rises in both numbers and colonized area. As isolated patches grow, they merge into uniform area but new distant patches emerge too.



Local population gradually continues its colonization. At this time, about 1/3 of the area is disturbed. If this piece of land represented one grid cell, this would be the statistical threshold of significant disturbance for me.

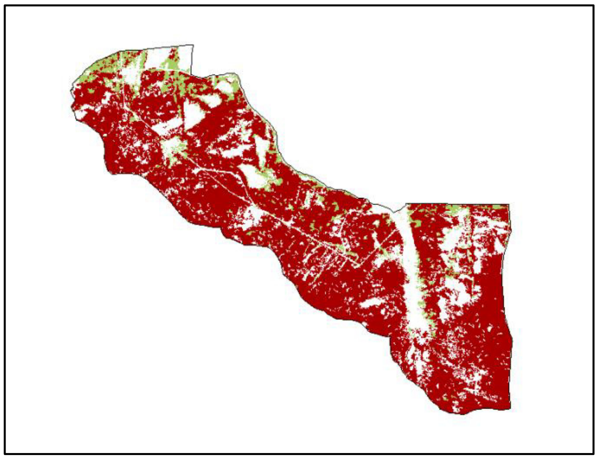
1998: Strong-perennial gradation



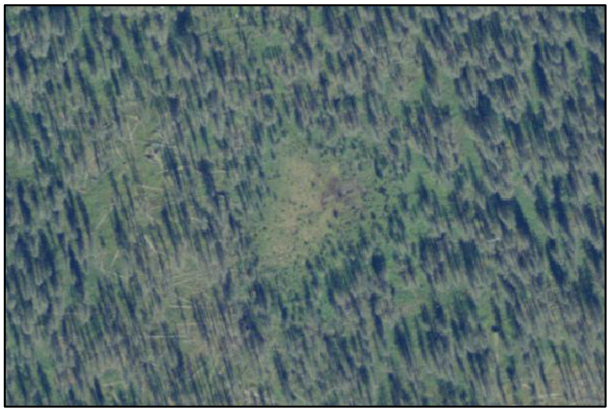
Bark beetle population is probably at its peak. With some exceptions most of the study area is already disturbed and only some small patches of living spruces mostly in the north remain.

Once bark beetle crosses certain thresholds and the environmental conditions are favourable, massive infestation usually occurs. At this point, almost 100 % of spruce trees around the peat bog were already successfully attacked and died.

2000: Post-collapse period



The population gradation of the bark beetle is literally at its end. It has only two imaginary choices: to disperse northwards away from the study area or perish due to lack of resources.



Disintegration of the tree layer is gradual and needs time. Dead trees remain in the upright position for years after successful infestation. In the area where the infestation started, however, first lying trunks can be distinguished.

Table 2: Aerial photos showing the further development of the peat bog site from 2010 and 2015.

The peat bog in 2010 & 2015	
	
About 20 years after the initial infestation and more than 10 years after the collapse the ratio of standing and lying dead trees is switched. Falling trees create space for newly emerged generation of spruce forest.	Current situation at the site. Almost all of the dead trees are fallen and new natural forest is well established due to self-regulatory processes. Trees grow at irregular arrangement and their differences in size indicate various age.

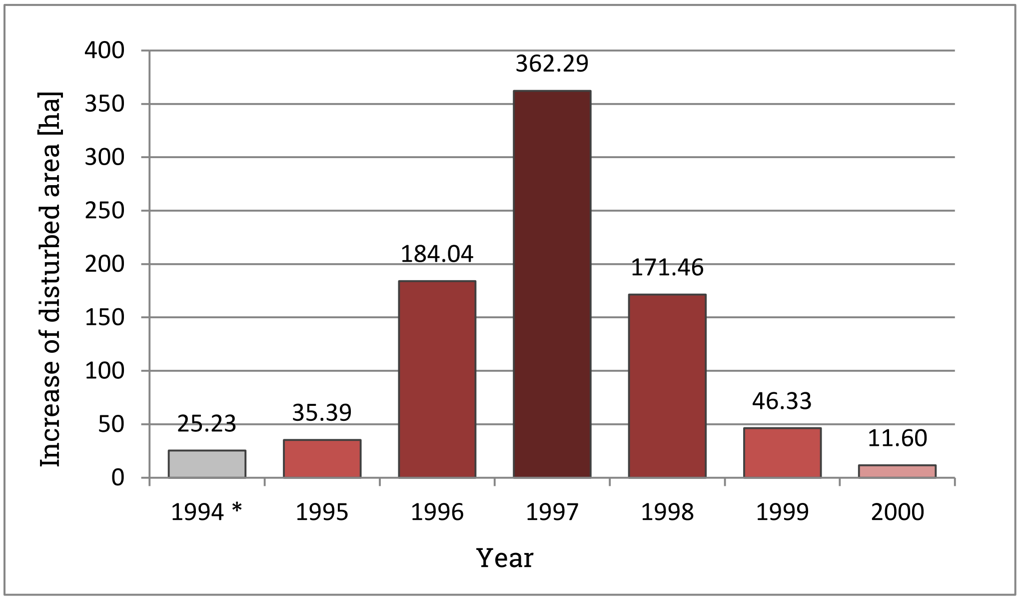


Figure 14: Yearly increase of disturbed area in hectares (value of 1994 is divided by 3).

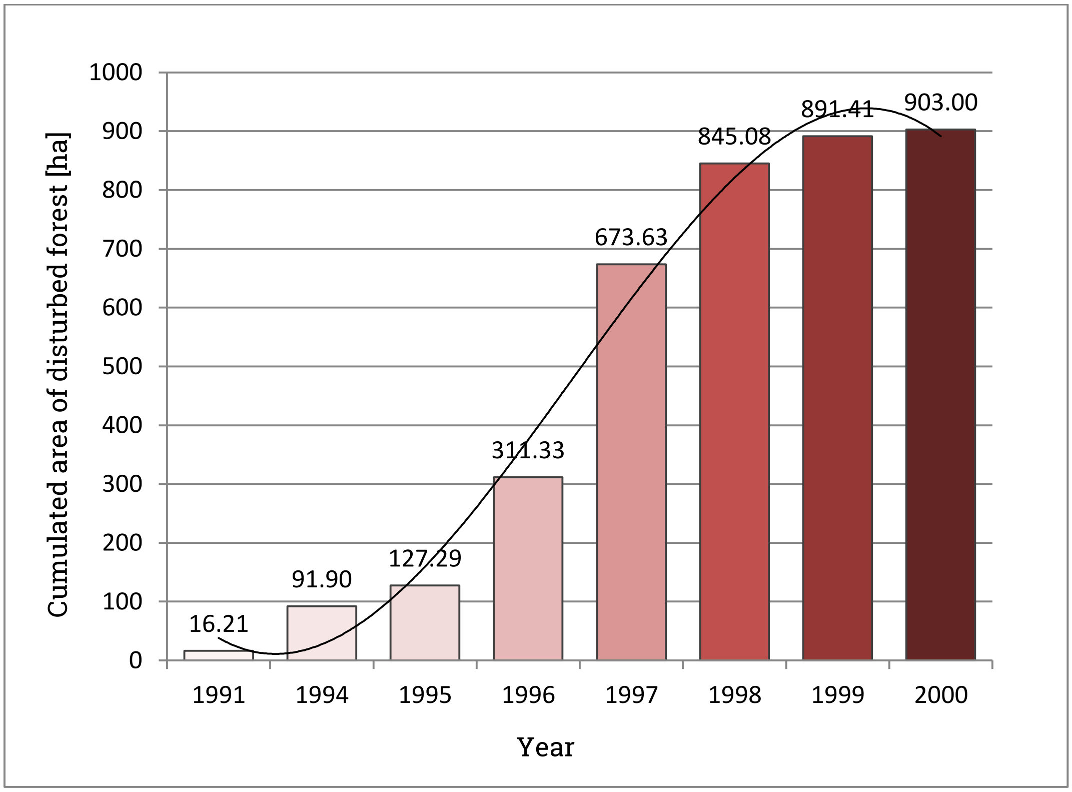


Figure 15: Cumulated area of disturbed forest.

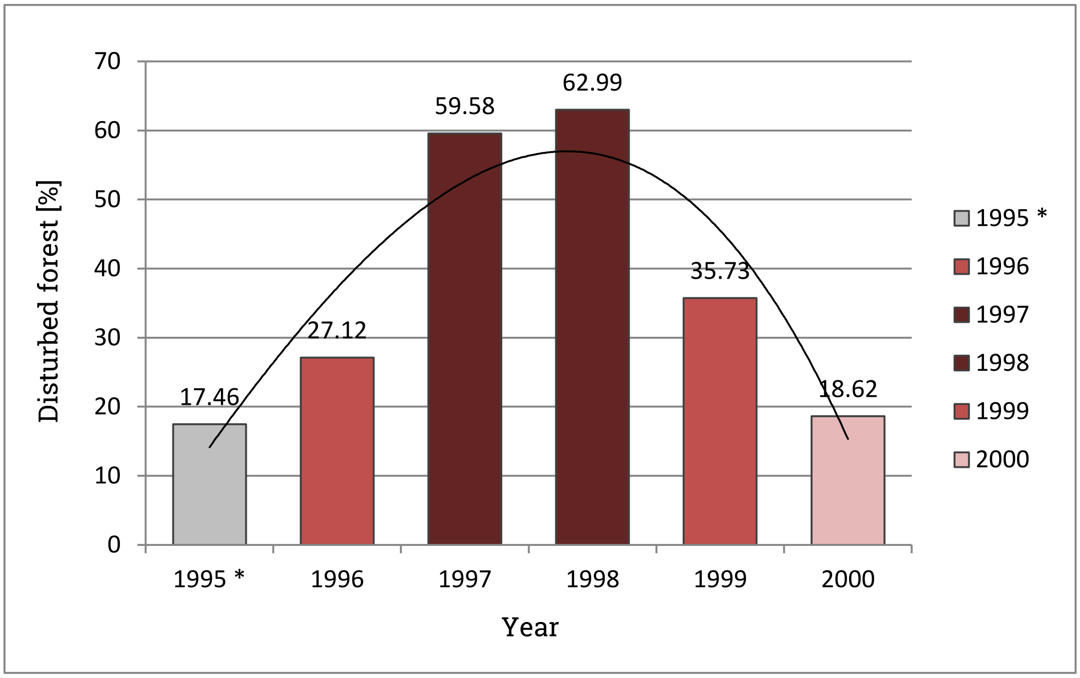


Figure 16: Percentage of potentially disturbable forest (grid cells) actually disturbed.

5.2 Weather data

The interpretation of the spatio-temporal model of changing land cover presented above would be hardly possible without the knowledge of the broader context – especially the weather conditions in given time and space. Therefore I obtained the data from CHMI related to the study area from years 1990 – 2000 which I present below. For more information about the source, the way how the data was originally measured etc. see Methodology (4.3).

5.2.1 Temperature

One of the main components constituting the weather is temperature, which is generally considered one of the most important conditions affecting the bark beetle population dynamics too. While the informative value of the mean temperatures is only limited (Table 3), also important extreme (Table 5) and cumulative values (Table 4) are presented and put into relation with data presented above (see Figure 17 and 18).

The analysis of temperature data shows the extreme nature of the study area. The mean temperature for the period 1990 – 2000 was only 1.74° C, while the yearly mean temperatures fluctuated between -0.07 in 1996 and 2.82° C in 2000. Logically very similar (but slightly different) pattern show the cumulated degree days presented in Table 6. The relatively warm season lasted usually from May to September, but even during these days the night temperatures occasionally felled below 0° C. The vegetation season[26] took from 0 to 3 months.

Table 3: Monthly and yearly mean temperatures for the period 1990 – 2000.

Description: first column represents months of the year while the first row the given years. Last row of the table contains the yearly means. Data cells contain mean temperatures in degrees of Celsius. The values are differentiated by colour based on their comparison with the mean (red: warm, blue: cold).

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[26] Vegetation season in this context is defined as the season with mean temperatures above 10° C.

	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
1	-6.62	-5.42	-4.64	-3.69	-3.79	-7.39	-9.3	-8.98	-5.21	-5.94	-8.9
2	-2.25	-10.48	-4.86	-9.78	-7.21	-1.78	-9.79	-3.5	-3.59	-7.58	-3.59
3	-0.27	-1.1	-2.35	-5.57	-0.53	-4.96	-7.44	-1.09	-3.41	-2.35	-1.99
4	0.08	-0.84	-0.97	1.68	-0.08	1.75	-1.01	-2.08	1.88	0.85	2.3
5	6.08	2.49	6.19	7.94	4.95	4.53	5.8	5.96	6.06	6.32	7.09
6	8.57	6.68	9.81	9.31	10.18	8.04	9.33	9.32	9.73	9.43	10.65
7	9.1	11.78	11.11	9.44	13.05	12.72	8.19	10.02	11.58	11.83	9.11
8	9.86	9.46	12.79	9.44	10.61	9.85	9.21	10.47	10.36	10.17	11.34
9	5.1	6.64	5.85	5.76	6.93	4.37	4.09	4.29	6.84	8.99	6.98
10	2.5	0.26	1.41	2.59	0.26	2.68	2.53	-0.24	4.14	2.76	5.49
11	-2.5	-2.83	-0.48	-5.59	1.33	-5.35	-1.74	-2.1	-4.86	-4.34	0.01
12	-7.16	-8.16	-6.37	-3.04	-2.92	-7.53	-10.67	-3.29	-6.88	-5.49	-4.7
YEAR	1.87	0.71	2.29	1.54	2.73	1.41	-0.07	1.57	2.22	2.05	2.82

Table 4: Cumulated temperature (degree days) counted for the period 1990 - 2000.

Description: the table shows so-called cumulated degree days counted for individual years of the given period. While the threshold was set up to 0° C, the information reflects the total sum of positive temperatures gained in given years. For more about degree days see Methodology (4.3.1.2).

Year	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**
Cum. T (DD)	1708	1609	1778	1776	1843	1665	1539	1685	1834	1856	1990

During the coolest part of the winter (typically in December or January) even the day temperatures don´t rise above 0° C during most of the days. What more, the night temperatures often fall under -10, -20 and occasionally even under -30° C. The number of days with minimum night temperature lower than -22° C fluctuated in given years between 6 and 26, while the longest row of these days fluctuated between 2 and 7 days. The minimum temperatures in given years were generally lower in the second half of the decade and fluctuated between -25.7 and -35.3° C. The snow covered the study area about 176 days per winter but this varied between 154 and 198 days.

Table 5: Winter temperatures and snow characteristics (1990 – 2000).

Description: the first column represents the given winter seasons while the others consecutively – the number of days with the min temperature under -22° C, max number of such days in row that occurred in the given season, the lowest temperature measured in the given season and the number of days with the continuous snow cover. The last row shows the means for the whole period.

Winter	Days min. -22° C	Days max. in row -22° C	Min. temp. [°C]	Days of snow cover
1990 - 1991	16	3	-27.6	158
1991 - 1992	6	2	-25.7	181
1992 - 1993	17	5	-27.9	189
1993 - 1994	10	5	**-31.7**	174
1994 - 1995	8	4	-26.2	154
1995 - 1996	26	7	-29.6	179
1996 - 1997	15	6	**-34.6**	171
1997 - 1998	10	7	**-31.3**	173
1998 - 1999	11	3	**-34.2**	198
1999 - 2000	13	4	**-35.3**	182
Mean	**13**	**5**	**-30.4**	**176**

5.2.2 Bark beetle degree days

Based on the knowledge of the bark beetle life and developmental cycle I was able to make a simplified temperature-based model related to the study area and the study period. As described in the Review (2.2.3.2), the whole lifecycle of the bark beetle is strongly temperature dependent. This contains especially two important aspects – the need for certain sums of cumulated temperatures (represented in degree days – for more see Methodology – 4.3.1.2) as well as certain thresholds that have to be exceeded in order to accomplish some tasks (e.g. the initial flight or the oviposition etc.).

In short, the degree day sums and thresholds used in tables below are as follows: 8.3°C for development, 11.4° C for oviposition (+ day length > 14.5 h), 16.5° C for flight (+ no snow cover); 140 cumulated degree days counted from 1st April (with temperature threshold at 0° C), 334 DD for development from egg to pupa, 557 DD for the whole developmental cycle and 277 DD for regeneration feed necessary for the sister brood.

Table 6: Data representing calculated cumulative degree days based on min and max day temperatures in given years (1990 - 2000) related with the bark beetle ecology and the following consequences (e.g. dates of the initial flights etc.).

Description: the whole table is structured into rows representing individual years (1990 - 2000). First block shows the information about the date of the first day in the given year when 3 basic conditions for initial flight of the bark beetle were hypothetically met – reaching the sum of 140 DD from 1st April, max temperature at least 16.5° C and no snow cover. The second block is represented by calculated degree days for the remaining part of the year beginning with the day taken from the first block (i.e. the potential initial spring flight). Third block takes the value from the first block and confronts it with the sum of degree days necessary for the development to pupa stage and maturation respectively. It also contains the information about the balance when the degree day from the next spring (before the next potential initial flight) is added. In general, negative balance means that the beetles wouldn´t be able to finish the development, according to the model. Last block represents information about sister broods – the first column contains dates of the second flight which leads to establishment of the sister brood. The second column confronts the sum of cumulated degree days necessary for development to pupa stage with the actual sum of degree days calculated for the period after the establishment of the sister brood until the end of the year.

Initial flight		**Cum. DD**	**BB development [DD]**			**SB thresh.**	**SB develop.**
>16.5°C, 140 DD		> 8.3° C	To pupa	To mature	+ Spring	227 DD	334 DD
1990	10. 5.	417.90	83.90	-139.10	-118.17	2. 8.	-192.6
1991	31. 5.	421.24	87.24	-135.76	-112.73	8. 9.	-334.0
1992	15. 5.	522.20	188.20	-34.80	14.28	23. 7.	-62.1
1993	9. 5.	451.05	117.05	-105.95	-75.31	27. 7.	-157.2
1994	16. 5.	536.92	202.92	-20.08	33.51	19. 7.	-58.5
1995	24. 5.	461.26	127.26	-95.74	-66.16	24. 7.	-131.5
1996	15. 5.	346.26	12.26	-210.74	-174.44	2. 8.	-247.6
1997	15. 5.	447.43	113.43	-109.57	-73.27	5. 8.	-152.8
1998	8. 5.	480.54	146.54	-76.46	-46.87	21. 7.	-121.3
1999	19. 5.	516.31	182.31	-40.69	-4.49	20. 7.	-77.3
2000	7. 5.	551.55	217.55	-5.45	> 0	10. 7.	-61.9

Although the model has been based on information from verified sources and also the temperature data were measured directly at the study area, it’s clear that the results don’t correspond with the reality. This is discussed in the Discussion (6.2.3.1).

The results of the model presented in Table 6 show that conditions suitable for the first flight of the bark beetle occurred each year during the May. Surprisingly, the cumulative sum of degree days received in every given year was insufficient for the full maturation of the beetles, according to the model. When the cumulated sum of degree days before the first flight next year would be added to the sum from the actual year, the threshold of the full development would be hypothetically surpassed only in 3 years – 1992, 1994, 2000. On the other hand, in all the years the temperature would be at least sufficient for reaching the pupal stage. Although, the establishment of the second generation in conditions of the study area is inconceivable, the establishment of one sister brood is possible. It could happen in all of the years except 1991 due to limitation by the day length. The sum of degree days needed for the development at least to the pupal stage would be never reached, however, by these beetles. The effects of temperature thresholds for the second flight as well as the oviposition and the long lasting snow cover were not significant.

5.2.3 Precipitation

Data about the precipitation in form of snow have been partly presented in Table 7 above. Nevertheless, it is important to note that not only the length of the period of snow cover is important but also its thickness. This, however, certainly differs in different parts of the study area and significantly varies during the season as well. In general, the thickness measured at the site in Luzenské údolí (i.e. at treeless area) was usually at least 50 cm but sometimes up to 250 cm and exceptionally even more during winters in the given period (1990 – 2000). I devoted a particular attention to investigation of the snow presence and the thickness of its layer during the exceptionally frosty days (with minimum temperatures under -22° C) and I have to state that the layer was always at least 50 cm and often even much more.

Focused on the precipitation in general, the average for the period 1990 – 1999 is 1 683 mm per year. Yearly means lower than 1 500 mm were measured only in 1991 and 1996. The precipitation considerably varied within the seasons and between the individual months as well. Monthly means for the given period varied between 98 and 185 mm. The minimum precipitation of 22 mm occurred in January 1997. On the other hand, next month it was 298 mm which makes it the snowiest February from the whole study period and one of the snowiest/rainiest months in general.

Table 7: Monthly and yearly precipitation means in millimeters (1990 - 2009).

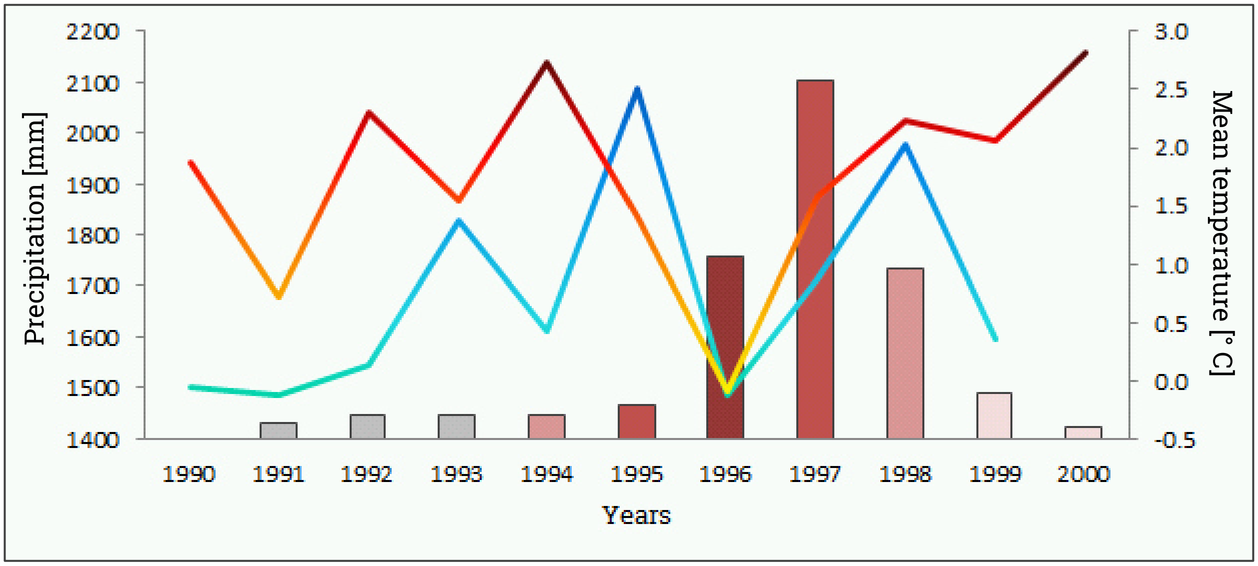

Figure 17: Synthesis of information about mean temperature and precipitation with data representing the total disturbed area in the given years (1990 - 2000).

Description for the figure below: the graph represents the mean temperatures (yellow/red line) and the total precipitation (blue line) combined with data about the newly occurred disturbance (columns). Disturbance data from 1990 are missing as well as the precipitation data from year 2000. Disturbance data related to 1992, 1993 and 1994 are represented by the cumulated value divided by 3.

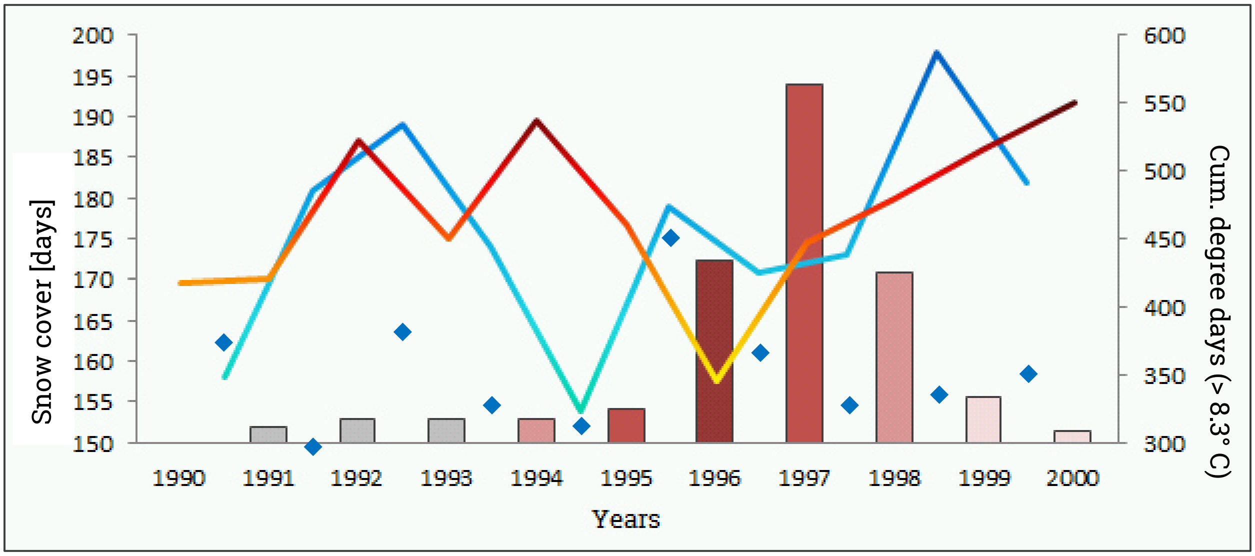

Figure 18: Similar graph as the previous one – only the precipitation was exchanged by the length of the snow cover and temperature by cumulated degree days. Blue rhombuses represent number of frost days with min. temperature under -22° C.

5.3 Infestation pattern analyses

One of the most potent factors used for explanation of future progress of bark beetle outbreak is the infestation pattern in previous year. While it's not possible to identify the patch or patches where the beetles flew from (using remote sensing methods), it's still possible to identify the nearest potential source at least. Following information served me as the background for the later derivation of KI.

5.3.1 Number of newly established patches

As a side effect of measuring the distance between newly established patches of disturbed forest and their nearest potential infestation sources the analyses gave me the information about the actual numbers of newly established patches. Of course I couldn't get this information regarding 1991 because I don't have any data from 1990 so I couldn't distinguish between old and new patches identified in this year. Similarly the data related to 1994 has only disputable explanatory value while it actually represents a cumulative value for years 1992 – 1994.

Table 8 shows that the number of individual patches newly established at the study area during 1995 – 2000 varied between 131 and 646. The size of these patches, however, changed significantly in respective years, which is shown in Table 9 on the next page to some extent. The information in this table probably better represents the bark beetle outbreak gradation while it represents the number of patches divided by the grid and merged within each individual cell. Logical consequence of this approach is the multiplication of large patches (because they cover significantly more than one grid cell) and underestimation of the small ones (because when divided, these fall below the limit 300 m^2). Anyway their numbers varied greatly between 170 and 3 664.

Table 8: Number of newly established patches of disturbed forest.

Description: each cell contains two numbers: before the slash – number of newly established patches (> 300 m^2) from the whole area; after the slash – the same thing but from the area reduced by 100 m buffer zone around the border of the study area and around land cover category "no data". In case of 1994 the buffer zone was extended to 200 m.

Established in:	1994	1995	1996	1997	1998	1999	2000
NEW PATCHES	594/388	409/359	646/491	435/358	404/342	242/189	131/89

Distance to nearest potential sources

It was of major importance (for statistical as well as for KI purposes) to estimate the usual bark beetle's dispersion radius which I, as stated above, tried to accomplish by measuring the closest distance between newly established infestation patches and their nearest potential sources. As indicated in Table 9, the vast majority of these sources were located closer than 100 m. The average number for years 1995 – 2000 and the given limit is 96.6 %, whereas almost 50 % of them emerged directly next to their nearest potential sources. It's also worth noting that although the dispersion pattern was unique in all years, year 1996 was kind of exceptional in both variables discussed.

Table 9: Statistics regarding the nearest source identified for each newly established infestation patch in each of the given years.

Description: data rows of the table show one after another: 1) total number of grid cells with significant disturbance, 2) share of these cells whose actual infested area was directly adjacent to the nearest possible source of infestation from the previous year, 3) the distance at which the newly established patches reached their nearest potential sources in 95 % of cases, 4) the longest distance identified between newly established patch and its nearest potential infestation source, 5) same as in point 2, only the distance was sat from 0 to 100 m, 6) percentage of grid cells with distance between the currently infested area and the nearest possible source beyond the limit 100 m.

Data from:	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**
NEW PATCHES	742	387	1 589	3 664	2 200	596	170
DIST = 0 [%]	10.65	56.07	24.29	42.88	43.41	58.39	60.00
95 % IN: [m]	201	66	113	66	71	48	74
100 % IN: [m]	359	241	348	258	304	147	354
DIST = 100 m [%]	94.88 *	**97.42**	**92.57**	**98.74**	**98.18**	**98.66**	**95.88**
DIST > 100 m [%]	5.12	2.58	7.43	1.26	1.82	1.34	4.12

Average distance values measured between newly established patches and their nearest potential infestation sources are presented in Figure 19 and Table 10 below.

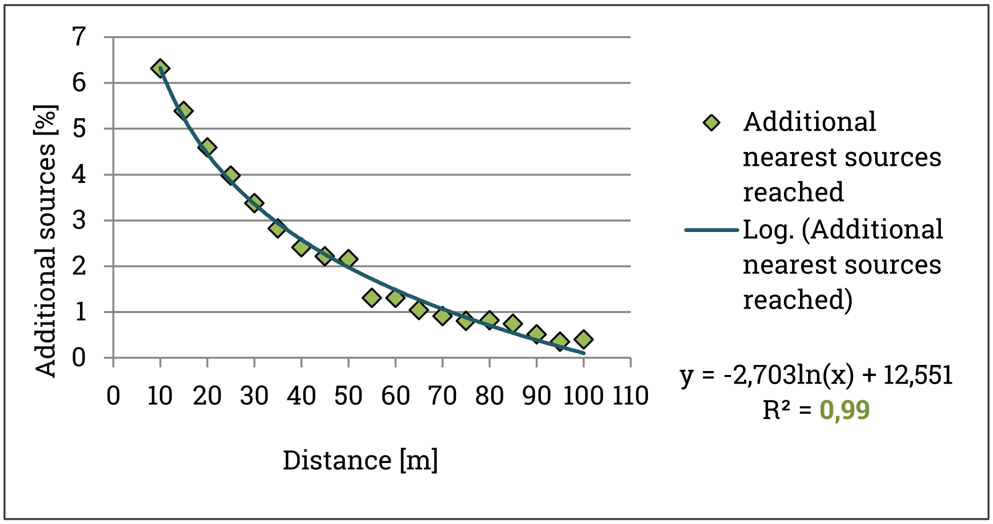

Figure 19: Graphical expression of data from the last column of the following Table 10 (distance range from 0 to 5 m was excluded).

Description (for the Figure XY above): Data distribution (green rhombuses) is expressed in addition by logarithmic curve (blue line). Formula of the curve is given (including R^2 value). X-axis represents distance ranges [m], Y-axis represents increase in numbers of nearest potential sources located in the given distance range [%]. The graph is based on data from 1996 to 1999 (1991 and 1994 are missing due to incomplete data series; 1995 and 2000 were excluded due to insufficient amount of data in datasets from these years).

Table 10: Statistics regarding the nearest potential source identified for each newly established infestation patch in each of the given years (1996 – 1999).

Description: each row contains values related to given years regarding the distance range [m] in which the nearest potential infestation source is located. Data from each year are represented by both, the absolute number of values measured (column ND) and corresponding percentage value. Last column provides information about average values for the distance ranges given.

DIST.	**1996**		**1997**		**1998**		**1999**		**MEAN**
	ND	**ND [%]**	**ND**	**ND [%]**	**ND**	**ND [%]**	**ND**	**ND [%]**	
0 - 5	483	**30.42**	1873	**51.15**	1147	**52.21**	412	**69.13**	**50.72**
5 - 10	595	7.05	2170	6.74	1301	6.92	445	4.53	6.31
10 - 15	689	5.92	2417	5.95	1453	5.96	472	3.69	5.38
15 - 20	781	5.79	2635	4.81	1584	4.55	494	3.19	4.58
20 - 25	866	5.35	2811	3.69	1684	3.82	513	3.02	3.97
25 - 30	936	4.41	2946	3.09	1768	3.64	531	2.35	3.37
30 - 35	1011	4.72	3059	3.14	1848	2.41	545	1.01	2.82
35 - 40	1075	4.03	3174	2.18	1901	1.91	551	1.51	2.41
40 - 45	1128	3.34	3254	1.91	1943	2.09	560	1.51	2.21
45 - 50	1190	3.90	3324	1.77	1989	1.59	569	1.34	2.15
50 - 55	1227	2.33	3389	1.23	2024	1.00	577	0.67	1.31
55 - 60	1267	2.52	3434	1.15	2046	1.05	581	0.50	1.30
60 - 65	1304	2.33	3476	0.76	2069	0.91	584	0.17	1.04
65 - 70	1334	1.89	3504	0.82	2089	0.91	585	0.00	0.90
70 - 75	1364	1.89	3534	0.60	2109	0.73	585	0.00	0.80
75 - 80	1391	1.70	3556	0.60	2125	0.46	585	0.50	0.81
80 - 85	1426	2.20	3578	0.30	2135	0.46	588	0.00	0.74
85 - 90	1446	1.26	3589	0.41	2145	0.36	588	0.00	0.51
90 - 95	1457	0.69	3604	0.38	2153	0.32	588	0.00	0.35
95 - 100	1471	0.88	3618	0.38	2160	0.32	588	0.00	0.40
SUM	1588	**92.63**	3662	**91.07**	2197	**91.62**	596	**93.12**	**92.11**

In General, cumulative character of data from 1994 means they have different distribution which is more gradual and stretched over a longer distance. It’s logical that the most extreme distance has moved further (to 359 m exactly, which is shown in Table 9) but even more important is the shift of 90 % and 95 % limits to approximately 175 and 200 m respectively which is roughly twice as far as 1996 – 1999 average. The data also doesn’t fit a logarithmic curve any more (it would have much more linear character).

Table 11: Statistics regarding the nearest potential infestation source identified for each infestation patch that occurred sometime between 1992 and 1994.

Description: Meaning of the individual columns is consecutively: percentage of all the nearest potential sources located max at the given distance, number of these sources, increase in number of these sources specifically for the given distance range, the same thing expressed by percentage.

DIST [m]	NS [%]	ΣNS	NS	INC [%]
0 - 5	**13.61**	**101**	**101**	**13.61**
5 - 10	17.79	132	31	4.18
10 - 15	21.16	157	25	3.37
15 - 20	23.85	177	20	2.70
20 - 25	27.22	202	25	3.37
25 - 30	30.86	229	27	3.64
30 - 35	34.10	253	24	3.23
35 - 40	36.93	274	21	2.83
40 - 45	39.62	294	20	2.70
45 - 50	42.86	318	24	3.23
50 - 55	45.69	339	21	2.83
55 - 60	49.19	365	26	3.50
60 - 65	51.48	382	17	2.29
65 - 70	53.37	396	14	1.89
70 - 75	55.93	415	19	2.56
75 - 80	59.03	438	23	3.10
80 - 85	61.59	457	19	2.56
85 - 90	64.29	477	20	2.70
90 - 95	66.44	493	16	2.16
95 - 100	68.06	505	12	1.62
100 - 105	70.35	522	17	2.29
105 - 110	71.97	534	12	1.62
110 - 115	74.53	553	19	2.56
115 -120	75.88	563	10	1.35
120 - 125	77.76	577	14	1.89
125 - 130	79.11	587	10	1.35
130 - 135	79.92	593	6	0.81
135 - 140	81.54	605	12	1.62
140 - 145	83.96	623	18	2.43
145 - 150	85.04	631	8	1.08
150 - 155	86.66	643	12	1.62
155 - 160	87.87	652	9	1.21
160 - 165	89.22	662	10	1.35
165 - 170	89.89	667	5	0.67
170 - 175	90.84	674	7	0.94
175 - 180	92.18	684	10	1.35
180 - 185	92.99	690	6	0.81
185 - 190	93.26	692	2	0.27
190 - 195	94.07	698	6	0.81
195 - 200	**94.88**	**704**	**6**	**0.81**

Table 12: Numbers of patches (grid cells) of potentially disturbable forest identified in the given years (1991 - 2000) and their actual state in the next year.

Description: First data row contains the number of potentially disturbable forest in form of grid cells (i.e. max 100 m distant from the nearest source of disturbance from the last year – in case of 1994 the distance is prolonged to 200 m and relates to data from 1991). Second row informs about the number of the grid cells from the first row that were actually disturbed (i.e. the disturbed forest on area min 300 m^2 occurred in them) next year. Third row gives the opposite information as the second row (i.e. the number of grid cells without occurrence of significant disturbance). The last row represents the percentage of how many potentially disturbable grid cells were actually disturbed (see Figure 16 for graphical representation of this). Values are differentiated by colours regarding the later use in GLM models (red: limiting value determining for large of the dataset used in GLM, green: larger group of observations which was later reduced by random choice).

Data from:	**1991**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**
POTENTIAL	-	6 373 *	5 184	5 999	3 361	1 570	843	485
DISTURBED	138 *	371	1 406	3 574	2 117	561	157	-
NOT DIST.	-	6 002	3 778	2 425	1 244	1 009	686	-
DIST. [%]	-	5.82 *	27.12	59.58	62.99	35.73	18.62	-

5.3.2 GLM models

Apart from the creation of the spatio-temporal model of the land cover change or the bark beetle dispersion respectively and its interpretation, the second major task of this thesis was an attempt to find out which factors actually affected the exact pattern of the infestation within individual years. For this purpose I decided to use statistical modelling – specifically the GLM models.

The Table 13 shows, that only models for years 1995 – 2000 were made. This is because of two main reasons – first, the 1991 model would be based on speculative foundations due to missing reference from 1990. Second, also the dataset would be very limited because the gradation was at its very beginning in 1991. Therefore I assume the explanatory value of the model would be very poor. On the other hand, I decided to include the 1995 model (although it is partly problematic as well).

Table 13: GLM models for the given years (1995 - 2000).

Description: each of the presented models consists of certain number of factors listed in order as I added them into the model step by step. The decision which factor should be added was based on AIC as well as the significant difference of a new model. This information is listed on sides of the respective factors in form of statistical outputs from ANOVA function that compared (in Chi-square test) all the length-variations of the model ("DEV" = deviance and actually reflects the AIC, while "SIG" = significance of model difference in comparison with other models, or the null-model respectively). In some cases also some other factors are added to the end of the list and printed in grey colour – these represent insignificant factors (with arrow) or factors that were significant but later excluded from the final model during diagnostic phase. The information at the bottom of the table means following: "H-L" – result of the Hosmer-Lemeshow test; "P.R^2 = pseudo coefficient of determination R^2; "D" = coefficient of discrimination. More about the presented GLM models can be found in Methodology (4.4.2). Here is the explanation of all the abbreviations used in the table: DEV – deviance, SIG – significance; sig codes: *** – 0.001, ** – 0.01, * – 0.05, . – 0.1; KI – kappa index, AGE – age, STO – stock density, NAT – degree of naturalness, EDA – edaphic category, GEO – geology, SOI – soil, LAN – land cover, DEA – dead forest, DEM – digital elevation model, SWI – saga wetness index, WI – wetness index, WET – wetness, COM – community, ASR – area solar radiation, PISR – potential incoming solar rad., HLI – heat load index.

DEV	**1995**	SIG	DEV	**1996**	SIG	DEV	**1997**	SIG	DEV	**1998**	SIG	DEV	**1999**	SIG	DEV	**2000**	SIG
334	KI	***	494	KI	***	1426	KI	***	202	KI	***	123	AGE	***	93	KI	***
70	GEO	***	158	AGE	***	157	NAT	***	91	AGE	***	74	KI	***	42	DEM	***
67	DEM	**	128	EDA	***	164	EDA	***	62	LAN	***	62	STO	***	24	EDA	***
22	STO	**	70	STO	***	93	AGE	***	52	NAT	***	47	SWI	***	13	COM	**
15	SOI	*	52	COM	***	67	STO	***	46	EDA	***	38	NAT	***	11	NAT	*
4	WI	*	34	NAT	***	67	SOI	***	31	STO	***	32	GEO	***	13	WET	***
14	EDA	.	28	GEO	***	42	LAN	***	31	ASR	***	19	DEM	***	4	SWI	*
8	NAT	*	13	WET	***	28	COM	***	21	COM	***	21	SOI	***	11	↑AGE	x
6	SWI	*	11	SOI	*	13	PIS	***	13	WI	***	8	PIS	**	6	↑STO	x
4	ASR	*	4	SWI	*	11	HLI	**	22	GEO	**	8	COM	**			
	↑AGE	x				11	WI	**	8	SWI	**	4	DEA	*			
						9	DEM	**	6	DEM	*	8	↑EDA	x			
						5	DEA	*	6	DEA	*						

H-L	0.604	0.482	0.075	0.292	0.051	0.925
P.R^2	0.530	0.254	0.306	0.171	0.273	0.460
D	0.585	0.309	0.364	0.212	0.328	0.533

Table 14: Statistics extracted from the GLM models with the KI as the only predictor.

Year	Coefficient	Std. Err.	Odd ratio	p-value	KI range	Probability
1995	0.8414	0.0601	2.3196	< 0.0000	5.07 - 13.72	2.30 - 97.15
1996	0.5225	0.0260	1.6863	< 0.0000	3.67 - 12.84	7.54 - 88.56
1997	0.6154	0.0195	1.8504	< 0.0000	3.95 - 14.15	3.32 - 94.82
1998	0.2992	0.0204	1.3487	< 0.0000	3.80 - 14.37	11.44 - 75.32
1999	0.3295	0.0342	1.3902	< 0.0000	3.08 - 14.17	6.09 - 71.46
2000	0.6832	0.0866	1.9802	< 0.0000	4.78 - 13.83	1.47 - 87.84

Table 15: Detailed GLM results concerning the Kappa index in the respective years.

KI	1995		1996		1997		1998		1999		2000	
	+	***	+	***	+	***	+	***	+	***	+	***

Table 16: Detailed GLM results concerning the age classes in the respective years.

AGE	1995	1996		1997		1998		1999		2000
4		-		-		+	*	-		
5		-		-	.	+		+		
6		-		+		+		+		
7		-		-		-		-		
8		+		+		+		-		
9		-		+		-		-	.	
10		+	**	+	**	+		-		
11		-		+	**	+		-		
12		-		+		+		-		
13		+		+	*	+	.	-		
14		+		+	*	+	.	-		
15		+	.	+	***	+		-		
16		+		+	*	+		-		
17		+		+	.	+		+		
18		-		+	.	-		+		
19				+	**	-		-		
20				+						

Table 17: Detailed GLM results concerning the stock density in the respective years.

STO	1995		1996		1997		1998		1999		2000	
1	+	*	+	*	+		+					
2												
3							+		+			
4	+		+	***	-	*	+		-			
5	+		+	***	-		+	**	-	***		
6	+	*	+	*	-	**	+	*	-	**		
7	+	*	+	***	-	*	+		-			
8	+		+	***	-	***	+		-	*		
9	+		+	***	-	**	+	*	-	*		

Table 18: Detailed GLM results concerning the degrees of naturalness in the respective years.

NAT	1995		1996		1997		1998		1999		2000	
2			+		+		+		+		+	
3	+		+		+		+		+		+	
4	-	*	+		+		+		+		+	
5			+		+		+		+		+	
6			+		+		+		+			

Table 19: Detailed GLM results concerning the edaphic categories in the respective years.

EDA		1995		1996		1997		1998		1999		2000	
K (normal acidic)	2	+		+	***	+	***	-				+	*
M (oligotrofic acidic)	3	+		+	***								
N (rocky acidic)	4	-		+	***	+	***	-					
P (acidic gleyous)	5	+		+	***	+	***	-				+	
Q (oligotrofic gleyous)	6	+		+	***	+	***	+				+	*
R (peaty)	7	+		+	***	+	***	-	*			+	**
T (oligotrofic waterlogged)	8	+		+	***	+		-	.			+	
V (wet)	9	+	**	+		+	**						
Y (extreme skeletal)	10	+		+		+	***						

Table 20: Detailed GLM results concerning the communities in the respective years.

COM		1995		1996		1997		1998		1999		2000	
Waterlogged s. f.	2			-		-	*	-	***			+	*
Peaty s. f.	3			+		+	**	-				+	**
Mosaic of w. & p. f.	4			-	***	-		-				+	

Table 21: Detailed GLM results concerning the soil types in the respective years.

SOI		1995		1996		1997		1998		1999		2000	
Glej zrašelinělý	1	-	.	-		+	*			+	.		
Ranker hnedý	2			-		-	***			+			
Podzol humusový	3	-		-	*	+	.			-	.		
Peaty soil	5	-	*	-	*	-	*			+	***		

Table 22: Detailed GLM results concerning the geology in the respective years.

GEO		1995		1996		1997		1998		1999		2000	
Aplite	1	-											
Granite	2	+	***	+	*			-	**	-	**		
Loam, sand, gravel	3			-				-		+			
Sandy-loamy to loamy-sandy sediment	5	+	*	+	***			-	*	-			
Mixed sediment	6	+		-				-	**	-			
Moor, peat, gyttja	7	+		+	.			+		-	***		
Syenite, diorite, tonalite	8			-						-			
Veiny granite	9	+	.	-	.			-	.	-			

Table 23: Detailed GLM results concerning the elevation in the respective years.

	1995		1996		1997		1998		1999		2000	
DEM	-	***					-	*	+	***	+	***

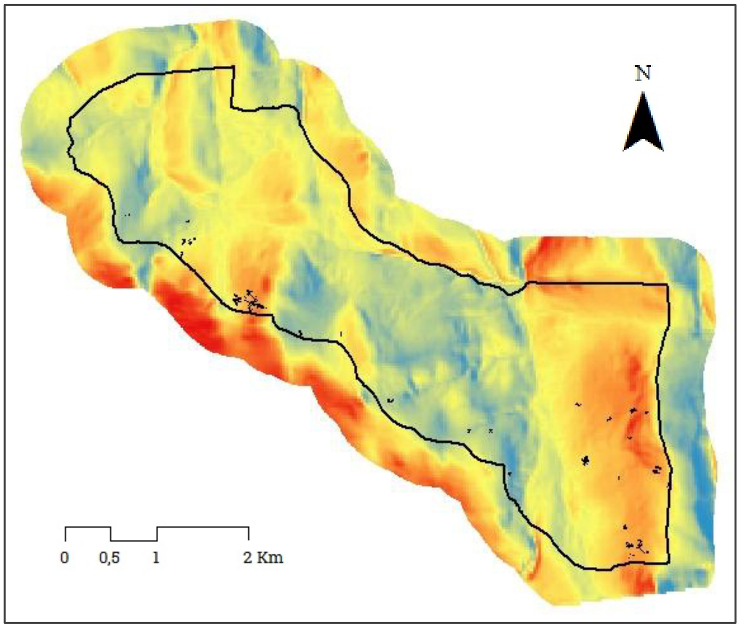

Figure 20: Map showing the HLI at the study area and its closest surroundings (250m buffer) and the largest disturbance patches present in 1991.

Description: the value of HLI (4474 - 9801) is represented by changing colours where blue is the lowest, yellow is the middle and red is the highest HLI. The study area is highlighted by the black line. The black spots are the biggest disturbance patches (> 900 m^2) identified in 1991.

6. Discussion

6.1 Vectorization

The change of land cover at the study area was documented during the study period (1991 - 2000) by aerial photography which is a logical and standard method used in such cases (e.g. Klobučar & Pernar, 2012). In the nineteen nineties, however, the remote sensing methods were not as advanced as today which meant certain limitations and resulted in relatively poor spatial accuracy of the images. Some of the images have been previously used e.g. by Kautz et al. (2011) or Lausch et al. (2011) but no major editing was reported. Therefore the necessity of relatively time-consuming post-processing was quite surprising. In spite of significant improvements, some inconsistencies in data persisted and couldn't be removed.

The phase of the manual vectorization was considerably time consuming as well. From this point of view, the possibility of some automated and cost-effective procedure based on digital image analysis would be helpful. This is clearly reflected in the policy of BFNP. In 2010, Heurich et al. (a team of BFNP employees) published a paper describing a semi-automated method of dead trees detection performed on the same aerial images as I used in my thesis. Although, the presented results seem promising, they admit the necessary condition for functionality of such method is a totally accurate image set which simply could not be achieved on the given dataset.

Another possible alternative is represented by satellite imagery. Various authors have used this approach and achieved interesting results either by using the RapidEye (Ortiz et al., 2013; Osberger et al., 2013), Landsat TM/ETM+ (Latifi et al., 2014) or different scenes. Nevertheless, the spatial resolution of standard and freely available satellite imagery was insufficient for my needs. With this in mind, I decided only to become compatible with the Landsat data and based the statistics on grid of 30 x 30 m (which later showed as relatively farsighted). In comparison, Lausch et al. (2011) chose a finer scale represented by a grid 20 x 20 m, but achieved just comparable results.

6.2 Bark beetle outbreak

It is evident that the source of the bark beetle infestation came to the study area from the east and the south west from across the national border just at the beginning of the nineteen nineties. This is in accordance with description of the bark beetle outbreaks in the nineteen eighties as well as the nineteen nineties in both ŠNP and BFNP as provided e.g. by Skuhravý (2002), Lausch et al. (2011) or Hais et al. (2008).

6.2.1 Infestation pattern on landscape level

Skuhravý (2002) mentions that according to analysis of aerial images from 1992, only individual dead trees and 12 larger patches of about 15 to 20 dead trees were present at the study area from Špičník Mountain westward along the border. This seems underestimated to me, while I have counted about 14 patches of approximately this size present at this part of the study area already in 1991. Additionally, I recognized another cluster of disturbed patches in south-east corner of the study area westward and southward from the mountain Velká Mokrůvka, which comprised of another 15 large patches in 1991. These findings are based on assumption that 5 trees correspond with area of about 300 m^2 – so patches described above had area of 900 m^2 and more.

It is evident that these two areas described above become the main sources for later dispersion. In general, my findings concerning the dispersion pattern are in accordance with statements provided by Skuhravý (2002), who describes three basic ways of bark beetle dispersion during the given outbreak as follows:

1) enlargement of the actual patches – mostly the larger sources,
2) establishment of smaller focuses usually not far from the large sources,
3) attacking of the individual trees or just small patches in more or less scattered pattern usually within longer distances (in radius of about 250 m).

The first point can be well documented by the fact that about 50 % of newly emerged patches were directly adjacent to the infestation sources from the previous year, according to my model. There was also a clear trend concerning the increase of relative number of adjacent patches from about 24.3 % in 1996 to 60 % in 2000 supporting the hypotheses of changing dispersion pattern as proposed by Wichmann and Ravn (2001). The statement from the second point is in accordance with my results as well while I have shown that during 1995 – 2000 the majority (> 95 %) of newly disturbed patches emerged in distance that varied from 48 to 113 m to the nearest source from the last year. This would be probably endorsed by Wermelinger (2004) who agrees that the bark beetle is able to fly at distances of several hundreds or even kilometres but as the radius of the higher risk considers only the distance < 100 m. Kautz et al. (2011) who analysed the dispersion of the bark beetle in BFNP during 1988 – 2009 report 66 % of newly established patches to be within the buffer of 100 m. Regarding the third point, I can't responsibly comment it while my model discriminates the individual trees as well as the smallest patches (> 300 m^2).

Anyway, as the time passed and the population gradation and dispersion progressed, the pattern was roughly as follows: the smallest patches and individual trees faded away or alternatively developed into significant sources. These, together with other large sources, gradually merged and later spread over the whole study area. This is in accordance with description of Skuhravý (2002) or Robertson et al. (2007) but reportedly in contradiction with statements of Schwenke (1996).

6.2.2 Disturbed area in individual years

The peak of the gradation came in 1997 when more than 360 ha of forest were disturbed in a single year, according to my model. The area of disturbed forest in individual years is probably the only point in which my findings significantly diverge from findings of Skuhravý (2002). He claims that the gradation culminated already in 1996. In his book, he describes the situation in the non-intervention zone which is roughly identical with the study area while estimating the total proportion of the disturbed forest to 80 % in 1996. Actually, this was only about 35 % of the total disturbed area (i.e. 311.33 ha) and even less of the total forested area, according to my results. Although a part of my image set from 1996 is missing, the no-data area could possibly explain max difference of about 5 %. The comparison of my results (see Figure 14) and the observations of Skuhravý are presented in the following Table 24:

Table 24: Comparison of data about area disturbed in individual years represented in percentage reported by Skuhravý (2002) and me (in this thesis).

Period	**1991 - 1994**	**1995 - 1996**	**1997 - 1998**	**1999 - 2000**
Skuhravý (2002)	22	61	12	5
Brož (2016)	10	24	59	6

As far as I know, other authors do not provide any objective data that could possibly bring some light into this problem. I find only one possible explanation for such significant difference – while Skuhravý (2002) based his information on the analysis of satellite imagery, his outputs had to be inevitably much less accurate than mine. Therefore what I have accurately marked as only partly disturbed forest could be hypothetically overestimated by Skuhravý (2002) and therefore marked as a totally disturbed forest. Similar problem from the same area describe Hais et al. (2008) who analysed satellite images covering both sides of the national border and considered their numbers significantly lower than those published by Heurich et al. (2001) or Skuhravý (2002). In my opinion, this typically illustrates the problematic nature of satellite imagery as discussed above or e.g. in Mosbech & Hansen (1994).

6.2.3 General conditions

The population gradation of the bark beetle and consecutive large-scale dieback of the forest can be interpreted at two main levels – stand and landscape. While at the stand level, the dynamic is considered to be mainly driven by various factors affecting the bark beetle and its environment (e.g. Raffa et al., 2008), the dynamic of the bark beetle at the landscape level is probably rather driven by factors and general conditions related to the area (i.e. the weather), respectively the forest (i.e. the health condition of the forest) or the bark beetle population (i.e. the occurrence of an initial disturbance), as a whole. While the last point has been already addressed, only the discussion about weather and some notes about other general conditions follow.

6.2.3.1 Weather

It is a part of a current paradigm that one of the main factors affecting the overall population dynamic of the bark beetle is the course of the weather (Grodzki et al, 2006; Skuhravý, 2002). The weather, however, is a relatively wide term and one simply cannot cover it by a single description. Therefore it is appropriate to divide the term into individual components and try to interpret them individually. Most of the authors attribute the biggest influence to the temperature.

Temperature

It is evident that the study area represents relatively extreme and hostile environment in terms of both – mean as well as extreme temperatures. On the other hand, the temperature situation is probably not as extreme as the presented results suggest. The long-term mean temperature for the larger area of Modravské slatě counted (but not published) by CHMI is about 2.7° C. The mean temperature for the period 1990 – 2000 based on temperatures measured directly at the study area is about 1.7° C, however. The difference probably cannot be caused by generally colder weather during the given period while for example the mean temperature for the whole Pilsen region was even by approximately 0.66° C higher than the long term average (1961 – 1990) during the given period, according to CHMI (CHMI, © 2016).

The temperatures measured at Březník are probably generally lower and exhibit significant deviations due to inappropriate exact location of the climatic station in Luzenské údolí[27]. The valley is well known for its exceptional climatic conditions and

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[27] The station has been positioned here as a part of a personal initiative of Mr. Vojvodík, a former employee of CHMI, who is also commonly known under a nick name "Frost hunter" which speaks for itself (Vojvodík, 2016 in litt.).

is considered a so-called frost pocket (Sádlo, 2001). From this perspective I admit that all the temperature data presented in Results (5.2.1) should be taken with caution and rather as an illustration than "hard facts". Interesting seems to be the possibility to calibrate the climatic data with temperatures measured within the research projects at other parts of the study area (cf. Hais, 2016), but this is beyond the means of this thesis.

With the limited informative value of the data in mind, detailed inspection reveals relatively big differences between the individual years. The first year of the study period was exceptionally cold which could negatively influence the transition of the infestation from the Bavarian side across the border. As described by Skuhravý (2002), even the bivoltine populations in lower elevations of the BFNP were not able to establish a second generation that year. Of course this is not the case of the study area while the populations here are strictly univoltine (Hlásný et al., 2011) but according to my temperature model, even the establishment and consequent development of a sister brood was probably the most problematic in that year. If I accept the hypothesis of Wermelinger & Seifert (1999) that the sister broods play a major role just in univoltine populations, this explanation of infestation slowdown generally observed at the beginning of nineteen nineties seems logical. The significant role of the temperature at the beginning of the population gradation in 1991 can also be well illustrated with presented HLI map which clearly shows that the two main infestation sources were clustered in the areas with the highest HLI values. The preference of sites like sun exposed slopes of mountains Velká Mokrůvka or Blatný vrch was described many times also by other authors (e.g. Anilla, 1969; Netherer & Nopp-Mayr, 2005).

Unfortunately, the development in 1992 and 1993 is unclear due to missing data but other authors who describe the situation in the given area agree that the gradation had a relatively slow onset (Lausch, 2011; Skuhravý, 2002). According to my temperature model, relatively favourable was the year 1992 and especially 1994. This is in accordance with Matějka (2011) who statistically analysed the temperatures from the meteorological station Churáňov which is about 15 km distant from the study site. According to his results, years 1992 and 1994 were the second and third warmest years from the period 1983 – 2010. Skuhravý (2002) agrees that these favourable conditions, especially in 1994, probably started the later massive propagation of the bark beetle. Speculative remains the influence of episodic warmings in the middle of the winters – especially those from the winter 1994/1995 (Matějka, 2011; Strnad, 2003). As presented in Figure 18, possible positive influence could be also brought by small number of exceptionally frosty days (< -22° C) and short period of snow cover during this winter.

Once the population gradation fully began, even the relatively cold period of the following years could not stop it. This can be well demonstrated on example of exceptionally cold year 1996 (mean temperature at Březník: -0.07° C) in connection with exceptional number of frost days in winter 1995/1996. Despite the hard conditions, the disturbed area increased dramatically that year and next year even more. This makes the previous explanations somewhat problematic, though. Nevertheless, according to Lausch et al. (2011) the influence of environmental factors changes with time and the actual phase of the population gradation so it is after all imaginable that the temperatures have a significant effect on the population dynamics at the beginning of the infestation while from the certain point (i.e. population density) it loses its importance.

Precipitation

Stress caused by insufficiency of water is commonly considered as one of the typical factors enhancing the susceptibility of Norway spruce to the bark beetle attack (e.g. Jakus et al., 2011; Netherer et al., 2015; Seidl et al., 2007;). On the other hand, it is often hard to distinguish whether the bark beetle outbreak has been facilitated by the drought or the associated high temperatures. Some findings suggest that the generally accepted role of the water stress could be actually overestimated (Christiansen & Bakke, 1997). Moreover, as already presented, the study area belongs to the rainiest places in the Czech Republic.

The analysis of the data shows some differences between individual years as well as within them but no clear connections with bark beetle population dynamics have been observed. Interesting is the co-occurrence of the extreme weather conditions in 1996 when the lowest temperatures met the highest precipitation from the given period. According to Grodzki et al. (2006) this combination was the key factor that ended the bark beetle outbreak in Tatra Mountains during 1993 – 1998. Nevertheless, no clear negative consequences at the study site have been observed.

When focused particularly on the snow – the interpretation of possible influence is unclear as well. The snow covers the study area usually almost for half of the year and probably substantially participates in the safe overwintering of the bark beetle in the soil litter (Faccoli, 2002). Based on the information provided by Košťál et al. (2011), it is hardly imaginable that the beetles or even larvae or pupae would survive the extreme frosts under the bark as described e.g. by Faccoli (2002) or Hrašovec et al. (2011). If I accept this assumption, it seems logical that the beetles overwintering in the soil litter would have to wait until the snow cover melts. It is surprising that I did not find any notice concerning this aspect in any source. Anyway, the possibility of limitation of the bark beetle by the snow cover was assessed using my temperature model and is considered to be of very little importance.

Wind

Another factor important especially regarding the bark beetle dispersion is considered to be the wind (Bayers, 2000). Unfortunately, there is no data available directly from the study area regarding this variable. This would be probably necessary for a deeper analysis, however. It is a part of common knowledge that the wind conditions may be highly variable depending on the exact time and space even within a relatively small area and short time period (e.g. Strnad, 2003). The main problem is that the bark beetle tends to fly in the both directions – along the wind as well as against it, depending on the actual speed of the wind as summarizes Skuhravý (2002). On the other hand, the fact is that the prevailing direction of the wind is in the direction of the documented bark beetle dispersion. Also the average wind speed in ŠNP (5 – 8 $m \cdot s^{-1}$ at the most exposed treeless areas and 1 – 2 $m \cdot s^{-1}$ in the deep valleys) presented by ŠNP (© 2008 - 2016) is relatively high and suggests rather the flights along the wind. Therefore it seems that the wind might play a positive role in the dispersion, although there is no evidence for this statement. This opinion has been approved also by Skuhravý (2002).

Another way how the wind can indirectly influence the bark beetle population dynamics is by affecting the heath condition of the trees. Exceptionally strong winds followed by windthrows are the well-known triggers of the bark beetle outbreaks (e.g. Økland & Bjørnstad, 2006) but they can act also in a less devastating way by just breaking the branches or the top parts of the trees (Bouget & Duelli, 2004). Similar effects can be caused by heavy snow or even the combination of both factors (Peltota et al., 1997). No mentions about such events have been reported from the study area in the given period, however.

6.2.3.2 Imissions & other factors

The heath condition of the forest depends on many variables of which the imissions are traditionally considered the most important in this area (e.g. Zatloukal, 1998). According to review by Zatloukal (1998), the negative influence of imissions in Bohemian Forest has been generally underestimated and overlooked in the past. It is possible that the rapid deterioration of the forest health condition was caused by the stress cumulated during the previous decades.

Imissions aside, Zatloukal (1998) describes many other types of historical anthropogenic stresses and disturbances that could affect the health condition of stands in the Bohemian Forest. Although he is rather more radical in his opinions than the scientific mainstream, the most of the authors agree that the onset of the bark beetle propagation and its success was probably facilitated by a whole wide spectrum of general conditions that even might possibly act in mutual synergy. At the end, it is also important to add that certain cases were documented in the past when the bark beetle had a similarly favourable conditions (i.e. the windthrows followed by dry and hot summers), but the outbreak did not occur. Skuhravý (2002) attributes this discrepancy to the inner factors (further unspecified) of the bark beetle population dynamics.

6.2.4 GLMs

Different authors have tried various approaches when modelling the bark beetles dispersion and infestation patterns or the probability of infestation depending on the numerous environmental factors respectively. Some of the statistical methods they have more or less successfully used include classification and regression trees – CART (e.g. Hilszczanski et al., 2006; Zolubas et al., 2009), ecological niche factor analyses – ENFA (e.g. Lausch et al., 2011), generalized linear models – GLM (e.g. Dutilleul et al., 2000; Kulla & Marušák, 2011; Liang et al., 2014) and others. I personally have considered all the three approaches named above but due to various reasons finally decided to realize only the GLM.

6.2.4.1 Differences between models

Although the rules used when including the factors were arbitrary to some extent, they had not been changed during the process, so the models are mutually comparable. The inspection of the results presented in Table 13 shows that the individual models differ significantly among the years. The length of the final models varies between 7 and 13 factors. The final form of models related to the situation in 1995 and 2000 has been probably influenced by the small datasets while at the beginning of the population gradation there were not many disturbance patches yet and in contrast, at the end of the gradation there were not many new disturbance patches already. This is probably the reason why the individual factors are generally less significant in comparison with other models (Pekár & Brabec, 2009).

The trend of decreasing pseudo-R^2 and discrimination coefficient up to year 1998 and later increase of these parameters in 1999 and even more in 2000 can be possibly interpreted in two ways. First, it could mean that the predictive value of the factors used in the analyses was changing in favour/disfavour of some other unknown and therefore unused factors. Second, it could mean that the importance of factors in the respective phases of the bark beetle population gradation was changing in general. Because the list of factors used in the analyses is relatively comprehensive and based on extensive literature research and the interpretations of some authors (e.g. Lausch et al., 2011 & 2013) are in accordance with the second hypotheses as well, this explanation seems more probable.

6.2.4.2 Factor composition

When taking also the insignificant factors into account, the factor composition in all the models shares a similar pattern. About half of the factors (specifically the KI, age classes, stock density, degrees of naturalness and edafic categories) are present in every model while the other half is variable. It is worth the note, that factors named above usually occupy the first positions in models from 1996 to 1999 (with some exceptions) whereas in the models from 1995 and 2000 they are scattered from the beginning to the end. The interpretation whether this could be due to small limitation of datasets described above or the composition of the models just reflects the different bark beetle preferences and population dynamics remains unclear to me. Lausch et al. (2011) describe the pattern observed at the beginning of nineteen-nineties on the Bavarian side of the Bohemian Forest and notice that the spread of the bark beetle was mainly driven by only a few dominant environmental variables mostly of biological-structural nature. Similarly Simard et al. (2011) attribute the higher importance to the tree and stand characteristics at the initial phase of the *Dendroctonus* sp. outbreak as well. This does not correspond with my data at all.

In general, my results regarding the similar pattern of the “core factors” in all models correspond with findings of other authors only to a limited extent. Lausch et al. (2011) did not find any mono-causal correlations between investigated factors and the bark beetle dispersion. On the other hand, they attribute generally much higher importance to distance from the infestation patches from the previous year than to the other factors which is in perfect accordance with my results. They also identified some factors with lower importance but relatively constant effect such as elevation, soil conditions or successional stage of the forest that occurred relatively often (among others) also in my models. It should be noted, however, that these results are based on a different statistical method and relate to a much longer period (18 years). General conclusions about relatively low importance of plot-level factors (e.g. stand structure or soil) make also Simard et al. (2011). This seems to contradict with my findings. On the other hand, they highlight the importance and a good explanatory value of landscape-level factors by which they mostly mean the factors representing the pressure of bark beetle. The importance of close distance between infestations in subsequent years is emphasized also by Kautz et al. (2011).

Many other authors investigated the influence of various factors as well but their results have often only low explanatory value because they usually do not pay attention to spatio-temporal development of the outbreaks.

6.2.4.3 Kappa index

Without any doubts, KI is the factor which achieved the best results throughout all models except year 1999 when it ended on the second place. Still it was the only one factor present in every final model and highly significant at the same time (Wald-test; $p > 0.001$). These results generally support the statements about very good explanatory value of the factors representing the spatial distribution of bark beetle infestation in the previous year (e.g. Kautz et al., 2011; Kulla & Marušák, 2011; Lausch et al., 2011 & 2013; Simard et al., 2011). In fact, the great difference in AIC between KI and the next factor included into each model (see Table 13 in Results) suggests that KI could be actually used as a single explanatory factor or predictor respectively if necessary. Some statistics regarding such models have been shown in Table 14. The probabilities of significant disturbance based just on the KI values covering wide ranges seem promising to me. The whole concept of KI, however, is not completely finished yet and deserves some further development. Therefore some ideas how to enhance the concept follow.

Some possible enhancements

Although the buffer zone of 100 m has been determined based on the empiric results and seems to fit at given time and space, it could be possibly significantly extended. This might be necessary when applying the index in different areas and overall conditions because various authors often report different distance values. While Kautz et al. (2011) or Wermelinger (2004) agree with me and see the critical distance at 100 m, some other authors report distances up to 500 m (e.g. Duelli et al., 1997; Faccoli & Stergulc, 2008). This would logically mean also the respective change of the basic equation of the index based on a different dataset.

Further, the absolute distance measured within the buffer could be possibly exchanged by a relative distance in my opinion. Some authors report that the bark beetle flight behaviour can be strongly influenced by its actual environment and other factors. Depending on the presence or absence of the forest or its structure (e.g. stock density) the length of the flight can significantly vary (Franklin & Grégoire, 1999; Skuhravý, 2002). Author who deals with the modelling of various aspects of the bark beetle flight and dispersion pattern on a long-term basis is J. A. Bayers (Bayers, © 1996 – 2014). From this perspective I find interesting an idea of building a cost layer. Such layer would be probably based on DEM and vectorised land cover but it could possibly include many other variables such as differences between natural and artificial treeless areas (Grodzki et al., 2006), the density of forest etc. As far as I know, nobody has already applied this approach.

Another aspect of KI, probably the least elaborated, is the penalization for directions not preferred during the dispersion. While the actual value (0.85) used in the current form of the index was derived from the empirical analyses of the dispersion pattern observed, it is far from being understood. I have hypothesized that the preference of north-east direction is a result of prevailing wind direction and/or the location of the primary source (in south) which was suggested also by Skuhravý (2002) but this needs some further investigation.

6.2.4.3 Forest characteristics

When focused on the core factors, it is clear that the whole group of forest characteristics achieved very good results. This includes age classes, stock density as well as degrees of naturalness. In general, these factors are among the most often investigated. They are also often accompanied by other stand characteristics such as diameter at breast height – DBH (e.g. Lausch et al., 2011; Simard et al., 2011; Zolubas et al., 2009) or the health condition of the trees (Jankovský, 2003; Netherer & Nop-Mayr, 2005). The data I obtained from forestry maps aside, there are some valuable data from the forest inventory and monitoring programme at the ŠNP available as well but these were not accessible for me.

Age

One of the basic approaches of mine was that I conducted the statistical analyses only with potentially disturbable parts of the forest. This criterion was based purely on the distance to the nearest infestation source from the last year. Nevertheless, I actually applied also the age filter by considering the stands younger than 21 years as the treeless areas. Other authors define the susceptibility based on the age of the trees as well. Trees of this age are usually considered potentially in a high risk regarding the bark beetle attacks (Netherer & Nop-Mayr, 2005; Skuhravý, 2002; Wermelinger, 2004).

When the respective Table 16 from my results is inspected, it does not show any clear patterns however. It seems that the preference of the bark beetle was changing throughout the given years and one cannot simply conclude that certain age classes were preferred in general. Only data from 1997 model show some significant preference of older stands. This is in contradiction with results of Kulla & Marušák (2011) who consider the age as a significantly good explanatory variable based in their results. This is the case of Netherer & Nop-Mayr (2005) as well, who concluded that the stands older than 60 years were clearly preferred. On the other hand, differently report Dutilleul et al. (2000) and Grotzki et al. (2006) who did not achieve any significant results regarding this factor. Similarly, Lausch et al. (2011) did not found any preference of older stands – moreover, they have proved the very opposite (although they tend to explain this by the lack of other relevant data).

Stock density

The interpretation of the results related to the stock density factor is unclear as well. In 1995, 1996 and 1998 the success rate of bark beetles attacks in less dense stands is obvious. On the other hand, in years 1997 and 1999 it is almost the very opposite.

The influence of the forest density on the bark beetle dispersion was investigated with the positive result by Jakuš (1998). This is in contrast with Dutilleul et al. (2000) and Kulla & Marušák (2011) who investigated the effect of this factor as well but did not achieve any significant results. Generally, much less is known about the effect of this factor than the effect of stand age, for instance.

Degrees of naturalness

Although no significance has been achieved regarding the results of individual degrees of naturalness, the pattern is obvious and the same in all years (except in 1995 which might be caused by the insufficient data). It seems that the categories with highest degree of naturalness are less likely to be successfully attacked by the bark beetle.This is in accordance with the common opinion expressed e.g. by Faccoli & Bernadinelli (2014) or Fischer et al. (2002).

6.2.4.4 Edaphic cathegories

Edaphic categories represent another factor based on the information derived from the forest maps. From the results inspection (see Table 19) it seems that almost all the categories in all the years when the factor has been included into the final model show a higher susceptibility to the bark beetle attack in comparison with the first category representing gleys moderately rich in nutrients. These results are especially highly significant in 1996 and 1997. On the other hand, the year 1998 is an exception and shows an opposite pattern because most of the edaphic categories show less occurrence of significant bark beetle attack in this model.

Kulla & Marušák (2011) are the only authors I found who have investigated this specific factor. They examined the role of six edaphic categories at one particular site in Kysuce region in Slovakia but did not get significant results. On the other hand, I assume that one of the main determinants of the edaphic categories is their trophic level. This should play an important role especially in the study area while it is generally poor in nutrients (Neuhäuslová, 2011). From this perspective the results make a relatively good sense. Because the reference category is the one with highest nutrient levels, the results (except year 1998) could be interpreted in the way that the deficiency of nutrients makes the trees more susceptible to the bark beetle attacks. This is relationship has been proven by Nef (1994) and Dutilleul et al. (2000) as well.

6.2.4.5 Comunity

The factor representing the prevailing forest community was significant in all the years except 1995. Its importance is not as high as of the "core factors" but the addition to the models is relatively constant. In 1999, the factor was not included into the final model because all the longer models did not pass the Hosmer-Lemeshow test. The reference category was represented by the montane spruce forests. Because the main driving force determining the present community here is the hydric regime and the montane spruce forests are considered the driest class, the results could be interpreted as the influence of the site wetness on the susceptibility to the bark beetle attack.

However, when the respective Table 20 in results is inspected, there are no clear patterns. It seems that in 1996 and 1997 the peaty spruce forests were more susceptible to the bark beetle attack while the waterlogged and the mixed spruce forests showed the opposite trend. In 1998 all the relatively wet communities (in comparison with montane spruce forests) showed fewer disturbances while in 2000 they showed significantly more disturbances. One could possibly try to interpret these inconsistent results using the precipitation in the respective years but due to lack of these data for 2000 and the fact that the factor was present only in 4 final models (including 2000) this is hardly achievable.

Anyway, the influence of a factor representing the soil moisture has been investigated by Dutilleul et al. (2000) with negative results. Another authors Kulla & Marušák (2011) investigated the hydric order of two different sites in mountainous regions in Slovakia as well. They have observed significant trends that were contradictory, however. These results suggest that there is no clear (mono-causal) relationship between the wetness of the site and its predisposition to the bark beetle attack. That is in relative accordance with results of manipulative experiments made by Christiansen & Bakke (1997) but in contradiction with Netherer et al. (2015).

6.2.4.6 Soil and geology

Various authors describe the possible effect of soil and/or geological substrata on the susceptibility of the spruce stands to the bark beetle attack (e.g. Skuhravý et al., 2002). As it is in case of other site characteristics (e.g. the hydric regime or the edaphic categories) it is thought to affect the spruce side of the bark beetle x spruce relationship. For example according to Lausch et al. (2011), deep compact layers of clay represent an obstacle for the spruce regarding the water supply and the penetration by its roots.

The inspection of my results (see Table 13) shows that at least one of these factors is included into every model except 2000. Although they do not play a major role, their contribution to the models is significant (especially in 1995). Because of correlation of these two factors only one of them is included in most of the models. Anyway, the detailed inspection does not reveal any obvious and simple relationships. The preference of the bark beetle changes in respective years and is hardly interpretable. There is not any single type of soil or geological substrata that would show the same result in every model.

Regarding the observations of other authors, Skuhravý (2002) describes the probable influence of different soil conditions in some parts of the study area during the bark beetle outbreak in the study period. Similarly Lausch et al. (2011) on the other side of the national border have found out that the sites where the intermediate or deep clay over compacted rubble was present showed the higher probability of bark beetle attack. Vavříček et al. (2005) and Dutilleul et al. (2000) consider the chemical components of soils as an important factor predisposing the Norway spruce to the bark beetle attack but did not addressed the question of individual soil types.

6.2.4.7 Other abiotic factors

A large group of factors that contributes to every model to some extent are factors based on DEM. Some of these factors (ASR/PISR/HLI) show relatively high correlation because they basically express the same thing. Nevertheless, I decided to include all of them because I wanted to compare their performances.

Elevation (DEM)

This factor has occurred in four models and it has been significant in 1997 as well, although it has not been included into the final model in this year. Interesting results have been achieved by this factor in the first and the last model of the study period when the elevation played the third and the second main role respectively. Interpretation of this fact seems relatively unclear to me.

One of the possible explanations could provide the topographic map which shows that the whole are is framed by local peaks while the central part has much more flat character. Therefore the elevation could be more important in the given years because the bark beetle colonized those areas at the beginning and at the end of the study period. On the other hand, this does not answer the question of switch in preference of lower elevation in 1995 and 1998 to higher elevations in 1999 and 2000. Another explanation seems to come from general conclusions about the spatio-temporal changes of the bark beetle dynamics as proposed by Lausch et al. (2011).

Anyway, the mainstream opinion is that the bark beetle preference is negatively correlated with elevation (e.g. Logan & Powel, 2001; Wulder et al., 2006). This is in general accordance with results of Lausch et al. (2011) as well as Dutilleul et al. (2000).

On the other hand, also the orientation of the hillside and its slope usually also play an important role which is stressed by some authors (e.g. Netherer & Nopp-Mayr, 2005).

ASR/PISR/HLI

All of these factors generally express the influence of temperature and heat. Although some authors report significant differences between the results achieved with these factors (McCune, 2007; McCune & Keon, 2002), I did not observe them at all. Interesting seems the difference between the probable relationship between HLI and the occurrence of the first infestation patches at the beginning of the outbreak (it is shown in Figure 20 and already discussed above).

Generally weak achievement of these factors is in relative contradiction with Netherer & Nopp Mayr (2005) who consider PISR as a very reliable indicator of predisposition as well as Mezei et al. (2012). Also Kautz et al. (2013) emphasize the effect of increased solar radiation (although they are mainly focused on a patch scale). Moreover, Mezei et al. (2012) also concluded that the effect of PISR on bark beetle preference does not change during the bark beetle outbreak which is in contradiction with my results as well.

7. Conclusions

This thesis aimed to several objectives. First, the spatio-temporal model based on aerial photographs has been made. It represents the changing land cover at the study area from the study period (1991 – 2000) which truly reflects the bark beetle population gradation and dispersion. Second, the model has been put into brother context, i.e. mainly weather conditions from the given time including the building of a simple temperature phenological model. Third, a comprehensive relational database comprising of various population-specific as well as habitat-forming factors that could play an important role in dispersion of the bark beetle has been built. Fourth, based on the results obtained from the spatio-temporal model, a new concept of a factor expressing the bark beetle dispersal potential has been proposed. Fifth, the data from the spatio-temporal model has been linked with the database and a GLM model has been made for each year from the period 1995 – 2000.

No direct evidence about the actual trigger of the bark beetle outbreak has been given, although it has been conclusively shown (based on a literature review and data from the beginning of the outbreak) that it was caused by the windthrows in 1983 and 1984 in the Bavarian National Park and later at the beginning of the nineteen-nineties spread to the study area. The onset of the bark beetle outbreak has been probably facilitated by the favourable weather but some other general conditions might play their role as well. The statistical analyses have shown that the most important factor throughout the years was Kappa index. The stand characteristics (age, stand density and degrees of naturalness) and edaphic categories complemented by the community type, soil & geology and factors based on DEM played more or less important role as well. Although some factors have shown constantly good results, detailed inspection has shown that their relationship usually cannot be considered as simply mono-causal. Not only has the significance of the individual factors changed during the outbreak but the way how they influenced the bark beetle dispersion as well. The results suggest that rather than the individual factors the combination of many factors in possible mutual interactions are decisive for the final bark beetle dispersion pattern.

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Apendix

List of abbreviations

AGE	Age
AIC	Akaike information criterion
ASR	Area solar radiation
BB	Bark beetle
BFNP	Bavarian Forest National Park
CART	Classification and regression trees
CGS	Czech Geological Survey
COM	Community
COSMC	Czech Office for Surveying, Mapping and Cadastre
CHMI	Czech Hydrometeorological Institute
D	Coefficient of discrimination
DD	Degree day
DEA	Dead forest
DEM	Digital elevation model
DEV	Deviance
EDA	Edaphic category
ENFA	Ecological niche factor analysis
FMI	Forest Management Institute
GEO	Geology
GLMs	Generalized linear models
H-L	Hosmer-Lemeshow test
HLI	Heat load index
INC	Increment
KI	Kappa index
LAN	Land cover
NAT	Degree of naturalness
ND	Newly disturbed
PIS/PISR	Potential incoming solar radiation
$P.R^2$	Pseudo coefficient of determination R^2
RMS error	Root-mean-square error
SB	Sister brood
SIG	Significance
ŠNP	Šumava national park
SOI	Soil
STO	Stock density
SWI	Saga wetness index
TWI	Topographic wetness index
WET	Wetness
WI	Wetness index

Table 25: List of geological substrata present at the study area taken from Pelc (1994). First two columns show information about all the categories stated in the geological map accompanied with their codes. Next two columns provide information about the category finally used within the project as well as about the change made.

Original category of geological substrata		**Category used in the project**	
Map Code	**Category**	**Category**	**Change**
6	Loam, sand, gravel	Loam, sand, gravel	-
7	Mixed sediment	Mixed sediment	-
9	Moor, peat, gyttja	Moor, peat, gyttja	-
12	Sandy-loamy to loamy-sandy sediment	Sandy-loamy to loamy-sandy sediment	-
1306	Migmatite	Migmatite	*Joined into one group*
1309	Migmatite		
1529	Aplite	-	*Excluded*
1536	Veiny granite	Granite	*Joined into one group*
1550	Granite		
1558	Granite		
1561	Syenite, diorite, tonalite	-	*Excluded*

Table 26: Phytocenological forest/woodland communities and their conversions into corresponding habitats. Biotope code used for biomonitoring purposes based on act no.114/1992 Coll. (Czech Republic, 1992). Next column provides the information about the classification of the biotope in European habitats directive 92/43/EEC. While the data was used to build a land cover layer also the conversion into CORINE land cover classification system is given. Last column of the table provides information about geobiocenological classification. All the information used for conversions between different classification systems comes from the Nature Conservation Agency of the Czech Republic (© 2007).

Montane reed spruce forests Phytocenological alliance: *Piceionexcelsae,* association: *Calamagrostiovillosae-Piceetum*				
Czech translation	**Biotope**	**NATURA 2000**	**CORINE**	**Forestry**
Horské třtinové smrčiny	L9.1	9410	42.23	8Y, 8N, 8M, 8K
Note: zonal, so-called climax, spruce (*Picea abies*) forests. For project purposes joined into one group with montane lady-fern spruce forests.				

Peaty spruce forests Association: *Sphagno-Piceetum*				
Czech translation	**Biotope**	**NATURA 2000**	**CORINE**	**Forestry**
Rašelinné smrčiny	L9.2A	91D0	44.A4, 42.23	7R, 8P, 8Q, 8T, 8G,8R

Waterlogged spruce forests Alliance: *Piceionexcelsae,* association: *Calamagrostiovillosae-Piceetum*

<table>
<tr><th>Czech translation</th><th>Biotope</th><th>NATURA 2000</th><th>CORINE</th><th>Forestry</th></tr>
<tr><td>Podmáčené smrčiny</td><td>L9.2B</td><td>9410</td><td>44.A4, 42.23</td><td>7R, 8P, 8Q, 8T, 8G,8R</td></tr>
</table>

<table>
<tr><td colspan="5">Mosaic of peaty and waterlogged spruce forests
Alliance: <i>Piceionexcelsae,</i> association<i>: Calamagrostiovillosae-Piceetum</i></td></tr>
<tr><th>Czech translation</th><th>Biotope</th><th>NATURA 2000</th><th>CORINE</th><th>Forestry</th></tr>
<tr><td>Mozaika rašelinných a podmáč. smrčin</td><td>L 9.2</td><td>-</td><td>44.A4, 42.23</td><td>-</td></tr>
</table>

<table>
<tr><td colspan="5">Montane lady-fern spruce forests
Alliance: <i>Athyrioalpestris-Piceion,</i> association: <i>Athyrioalpestris-Piceetum</i></td></tr>
<tr><th>Czech translation</th><th>Biotope</th><th>NATURA 2000</th><th>CORINE</th><th>Forestry</th></tr>
<tr><td>Horské papratkové smrčiny</td><td>L9.3</td><td>9410</td><td>42.23</td><td>8V</td></tr>
<tr><td colspan="5">Note: for project purposes joined into one group with montane reed spruce forests.</td></tr>
</table>

<table>
<tr><td colspan="5">Mountain pine bog woods
Alliance: <i>Oxycocco-Empetrionhermaphroditi,</i> association: <i>Pinomugo-Sphagnetum</i></td></tr>
<tr><th>Czech translation</th><th>Biotope</th><th>NATURA 2000</th><th>CORINE</th><th>Forestry</th></tr>
<tr><td>Vrchoviště s klečí</td><td>R3.2</td><td>91D0</td><td>44.A3</td><td>9R1</td></tr>
<tr><td colspan="5">Note: despite the name dominant tree species in this community is a bog pine (<i>Pinus x pseudopumilio</i>).</td></tr>
</table>

<table>
<tr><td colspan="5">Mountain pine bog woods with spruce
Alliance: <i>Oxycocco-Empetrionhermaphroditi,</i> association: <i>Pinomugo-Sphagnetum</i></td></tr>
<tr><th>Czech translation</th><th>Biotope</th><th>NATURA 2000</th><th>CORINE</th><th>Forestry</th></tr>
<tr><td>Vrchoviště s klečí a s expand. smrkem</td><td>R3.2</td><td>91D0</td><td>44.A3</td><td>9R1</td></tr>
<tr><td colspan="5">Note: bog pine (<i>Pinus x pseudopumilio</i>) but also spruce (<i>Piceaabies</i>) is dominant here.</td></tr>
</table>

Table 27: Database scheme. Range and/or description of individual factors is as follows: DISTURBED – disturbed/not disturbed = 1/0 threshold is at 1/3 of disturbed area = 300m^2; LAND – 1: > 90% living, 2: >10% dead; 3: > 10% treeless; 4: > 5+5% dead and treeless; WET - 0: < 90% wet, 1: > 90% wet; COMUN – range 1-4; NATUR – degree of naturalness (1 – natural, 6 – antrop.); STOCK – stocking density of the forest: 1 (min) – 10 (max); AGE – age classes 21-30, 31-40 etc., range 3-20; ASR – area solar radiation – sum for months 5-8; PISR – potential incoming solar radiation – sum for months 5-8; GEOL – geological substrata, range 1-8; SOIL – present soils, range 1-5.

MAIN FACTOR	**PARTIAL FACTOR**	**TYPE OF DATA**		**REFERENCE**
ID & MASK	ID			
	DISTURB	*binary*	*dynamic*	
LANDCOVER	DEAD	*continuous*	*dynamic*	
	LIVING			
	TREELESS			
	LAND	*cathegorial*	*dynamic*	> 90% living
BB	KAPPA			
HEALTH	WETNESS		*static*	
WATER	EDAPHIC		*dynamic*	G
COMMUNITIES/HYDRIC REGIME	MONT	*continuous*	*dynamic*	
	PEAT			
	WATER			
	MOSAIC			
	WET	*binary*		<90%
	COMUN	*cathegorial*		Montane reed spruce forest
CHARACTER OF FOREST	NATUR		*dynamic*	natural
	STOCK			densest
	AGE			21-30 years
HEAT, RADIATION	HLI	*continuous*	*static*	
	ASR			
	PISR			
TOPOLOGY	DEM	*continuous*		
	SWI			
SOIL & GEOLOGY	GEOL	*cathegorial*	*dynamic*	migmatit
	SOIL			h. podsol on par. and mig.

Table 28: Soil types of the study area

Soil type	Peaty gley
	Brown ranker
	Humic podsol on eroded
	Humic podsol on weathered paragneiss and migmatite
	Peaty soil

Table 29: Edaphic categories.

CODE	DESCRIPTION
G (1)	middle rich waterlogged ecological class (middle rich gley)
K (2)	normal acid ecological class (climax, oligotrophic species of herb layer)
M (3)	poor acis ecological class (poorest bedrock, raw humus)
N (4)	stony acid ecological class (poorer stony slopes and ridges – undeveloped brown soil)
P (5)	acid gleyous ecological class (acid pseudogley)
Q (6)	poor gleyous ecological class (poor pseudogley)
R (7)	peaty ecological class (transitional and raised bogs)
T (8)	poor waterlogged ecological class (poor peaty gley, limited growth of woody plants)
V (9)	moist, ecological class (springs, deluvia, flowing underground water)
Y (10)	extreme skeletal ecological class (poor, boulder rubble)

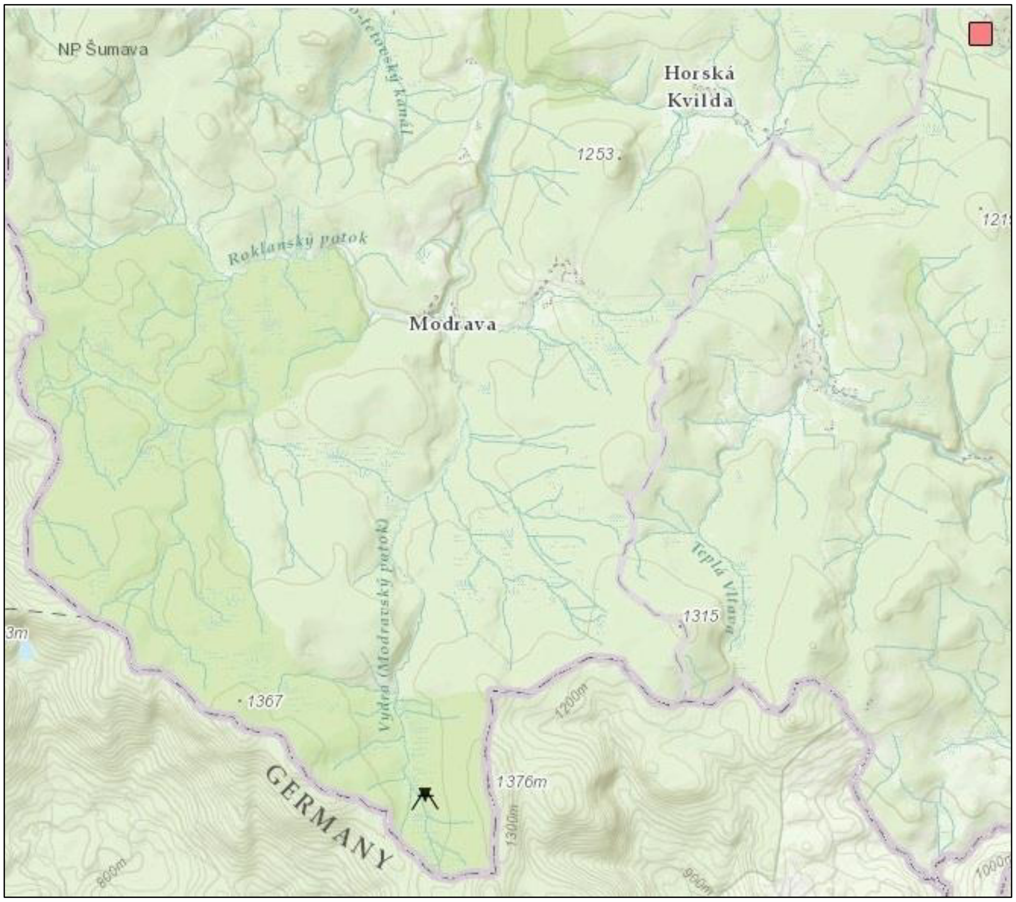

Figure 21: CHMI map detail (©CHMI [online]) of the study area and broader surroundings. Topographic layer shown above is based on ESRI WorldTopoMap service[1]. Two additional symbols important in terms of the project were added: first represents a totalizator located at Boundary-moor in Březník area. This automatic station serves only as a simple precipitation measuring device, although some other variables were measured nearby in the past including the examined years. Second symbol (pink square in the top-right corner) represents a 1st order hydro-meteorological station Churáňov. This station is permanently inhabited by a professional operator who measures the whole variety of climatic variables here.

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[1] Learn more at: http://www.arcgis.com/home/item.html?id=30e5fe3149c34df1ba922e6f5bbf808f

Fig 22: *Thanassimus formicarius* predates on bark beetle (www.uzsav.eu © 2016).

Figure 23: Recent picture of Březník area taken from the upper part of Luzný valley (approximate GPS coordinates: 48.9673694N, 13.4852128E). ©Vladimír Kunc.

Figure 24: Recent picture of site known as Novohuťské močály (approximate GPS coordinates: 48.9809133N, 13.4443508E).©Vladimír Kunc.

Figure 25: Hraniční slať (GPS coordinates: 48.9489289N, 13.4879033E). ©Vladimír Kunc.


Figure 26: Sand extraction and construction of a new road at Březník area. 1991 ©Zdeněk Uher.


Figure 27: Pile of sand and concrete panels at former Roklan reservoir. 1991 ©Zdeněk Uher.